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Influence of Weather on Breeding Success of Peregrine Falcons in the Arctic

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Many studies have examined the effects of weather on avian breeding success (e.g. Ojanen 1979; Wingfield 1984, 1988; Peach et al. 1991; Clarke and Johnson 1992; Hendricks and Norment 1992; Aebischer 1993; Sasvari and Hegyi 1993), but few studies have dealt specifically with raptors (e.g. Ridpath and Brooker 1985; Mearns and Newton 1988; Olsen and Olsen 1988, 1989a,b; 1992; Pietiainen 1989; Norriss 1995; Steenhof et. al. 1997). Similarly, breeding success of Peregrine Falcons (*Falco peregrinus*) has been studied throughout their range (see Hickey 1969, Cade et al. 1988), but only two studies have evaluated the effects of weather on breeding success (Mearns and Newton 1988, Olsen and Olsen 1989b).

We gathered data on 310 territorial pairs of Peregrine Falcons (*Falco peregrinus*) over 13 breeding seasons to explore the relationship between breeding success and weather. Specifically, we examined annual variability in breeding success and the extent to which breeding success varies with weather. We also examined weather and breeding phenology, as this relationship affected breeding success. The two previous studies of weather and breeding success in Peregrine Falcons (see above) took place in relatively benign climates. In contrast, the climate at our study area in subarctic Canada ranks among the coldest and harshest within the species' breeding range.

Study area and methods.—The study area surrounds the Inuit hamlet of Rankin Inlet (62°49′N, 92°05′W) on the northwest coast of Hudson Bay in the Northwest Territories. The 450-km^2 study area was established in 1982. The climate at Rankin Inlet is characterized by short, cool summers (July mean temperature 10°C) and long, cold winters. Strong winds are common, and summer storms usually start after the first week of August. The Inlet freezes completely in November and does not break up again until July. Snow cover lasts from late September to early June. The habitat is flat, treeless tundra interspersed with rocky outcrops of the Canadian Shield. These rocky outcrops have been shaped by glacial action to form a series of southwest-facing cliffs. The ledges on these cliffs provide most of the nesting habitat. Nests may be on oceanic islands, the coast, or inland. Eggs are laid in bowls scraped in the soil, or in old stick nests of Rough-legged Hawks (*Buteo lagopus*). The study population is migratory. Peregrine Falcons arrive on the study area in mid- to late May and lay eggs in the first week of June. The young fledge in mid-August and depart for the tropical Americas by late September. See Court et al. (1988a,b; 1989), Bradley and Oliphant (1991), and Johnstone et al. (1997) for additional details of the study population.

Data were collected from 1982 to 1994. The study area was thoroughly searched in mid-May each year. Most nesting sites were associated with an obvious growth of the lichen *Xanthoria elegens*, and an observer's approach to a territory usually elicited a defensive response from the resident pair. The flat, treeless topography made suitable cliffs easy to find such that more than 95% of the pairs were found prior to egg laying. Single birds on territories were not counted (and were quite rare). Nonlaying pairs were counted as territorial pairs if they were seen more than once and responded defensively to the observer. Nest visits during laying and hatching provided dates for the first egg laid and the first chick hatched. If the first-egg date was missed, it was estimated by subtracting the incubation period ($\bar{x} = 36.23 \pm$ SD of 2.29 days, $n = 44$) from the hatching date of the first chick. Each nest was monitored until fledging or nest failure. By continuously monitoring all nests, we avoided biases inherent in studies based on one or two surveys per year (Mayfield 1975, Steenhof and Kochert 1982).

Clutch sizes were based on territorial pairs so that proportion of pairs to lay and number of eggs laid could be incorporated into a single parameter. Egg mortality was calculated as clutch size minus the number of eggs to hatch. Sample size equalled number of laying pairs. Chick mortality was calculated as the brood size at hatching minus the brood size at fledging. Sample size equalled number of hatching pairs. Chicks were considered "fledged" at 25 days of age, even though the actual age at fledging was 35 to 40 days (see Steenhof and Kochert 1982:887). Chicks older than 25 days often wandered from the nest area and became difficult to locate.

Annual breeding phenology was established

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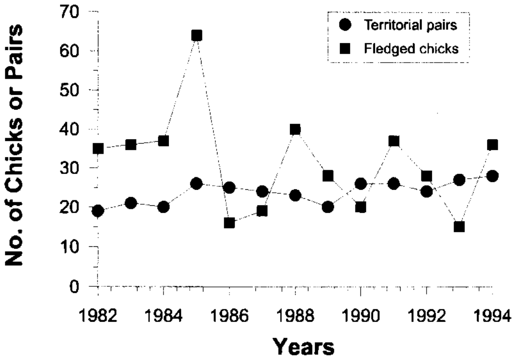

FIG. 1. Number of Peregrine Falcon chicks fledged (squares) and number of pairs holding territories (circles) at Rankin Inlet, 1982 to 1994.

based on the mean first-egg date. The breeding season was divided into the: (1) prelaying stage (21 days prior to first-egg date), (2) incubation stage (36 days starting on the first-egg date), and (3) nestling stage (21 days after the incubation stage). We used a nestling stage of 21 days because peregrines achieve thermoregulatory independence at this age (Enderson et al. 1972, Hovis et al. 1985).

Annual weather parameters were calculated for each of the three stages from weather data collected at the Rankin Inlet airport (the approximate center of the study area) by the government of Canada. Six variables were calculated: (1) mean daily temperature, (2) total snowfall, (3) total rainfall, (4) total precipitation, (5) number of hours with winds exceeding 15 km/h, and (6) number of hours with precipitation.

Results.—Over the 13 years of our study there were 310 occupied territories, of which 252 (81%) produced eggs, 197 (64%) hatched young, and 168 (54%) raised young to fledging age. On average, there were 24 pairs on territory each spring ($\bar{x}$ = 16 to 23 pairs/km^2 each year). An average of 13 pairs was left at fledging time. All breeders were adults, and as far as we know there was no mortality of breeders during the breeding season.

The number of territorial pairs increased from 19 in 1982 to 28 in 1994 ($r = 0.71$, $P = 0.01$, $n = 13$; Fig. 1). The total number of chicks fledged in the study area was much more variable than the number of pairs, ranging from 15 to 64 (Fig. 1). On average, territorial pairs fledged 1.4 chicks (0.6 to 2.5 per year), or 2.5 chicks per successful pair (1.8 to 3.1 per year). Unlike the number of pairs, there was no significant trend in numbers of chicks fledged over the course of the study.

None of the weather variables was correlated with the number of pairs establishing territories each year. The only weather variable that was significantly correlated with mean first-egg date was hours of wind ($r = 0.69$, $P = 0.01$, $n = 13$), but the relationship was dependent on a single year, 1987. Excluding data from 1987, the relationship was not significant ($r = 0.51$, $P = 0.09$, $n = 12$). Despite the lack of a linear relationship, the effect that heavy snowfall could have on egg laying was evident in 1987. A blizzard deposited 34 cm of snow between 31 May and 5 June 1987, completely covering potential nesting ledges and preventing laying. Snow melted from the ledges by 8 June, but the mean laying date in 1987 (20 June) was significantly later than that for the other 12 years combined (9.6 June ± SD of 4.16 days; $F = 17.93$, df = 1 and 11, $P < 0.01$).

Four weather parameters were significantly higher in 1987 compared with the mean for the other years (df = 1 and 11 in each case): total snowfall (31.2 cm vs. 3.12 ± 6.67 cm; $F = 15.86$, $P < 0.01$); total rainfall (19.2 mm vs. 5.80 ± 4.79 mm; $F = 6.99$, $P = 0.02$); total precipitation (57 mm vs. 11.76 ± 10.01 mm; $F = 18.85$, $P < 0.01$), and number of hours of wind greater than 15 km/h (317 h vs. 250.58 ± 25.86 h; $F = 6.09$, $P = 0.03$). June snowfall in 1987 was the highest on record (dating back to 1931).

Mean clutch size was negatively correlated with total snowfall and number of hours of rain during the prelaying period (Fig. 2). The combined effect of snowfall and hours of rain also was negatively correlated with clutch size (multiple linear regression, $R^2 = 0.71$, $P < 0.01$). There was no collinearity between snowfall and hours of rain.

Overall, there were no significant relationships between weather and egg mortality. In 1986, however, heavy snowfall caused some egg mortality. Fourteen cm of snow fell from 11 to 14 June 1986, and on 15 June we found a nest beneath 15 cm of snow. The parent had abandoned the nest by tunnelling through a snow drift. Rapid snowmelt prevented us from obtaining evidence from other nests, but in all, four pairs deserted their nests immediately, and another six pairs deserted later in the incubation stage. Egg mortality (number of eggs laid minus number of chicks hatched) was significantly higher in 1986 than in the other 12 years (2.26 eggs vs. 1.04 ± 0.33 eggs; $F = 12.44$, df = 1 and 11, $P < 0.01$). In 1986, total snowfall was the only weather parameter that differed from the other years (14.2 cm vs. 1.28 ± 1.70 cm; $F = 53.01$, df = 1 and 11, $P < 0.01$). Indeed, snowfall in June 1986 was the sixth highest on record for that month.

Although weather parameters were not significantly correlated with chick mortality, heavy chick mortality occurred after storms in 1987, 1990, 1992, and 1993. In 1987, three broods totalling seven chicks died after 50 mm of rain fell during a 7-day period. In 1990, five broods totalling 17 chicks died during a 4-day storm (69 mm of rain and 75 km/h winds). In 1992, virtually all of the precipitation during the nestling stage (30 of 31 mm) fell during a 3-day storm, killing 14 chicks in four broods. In light of this

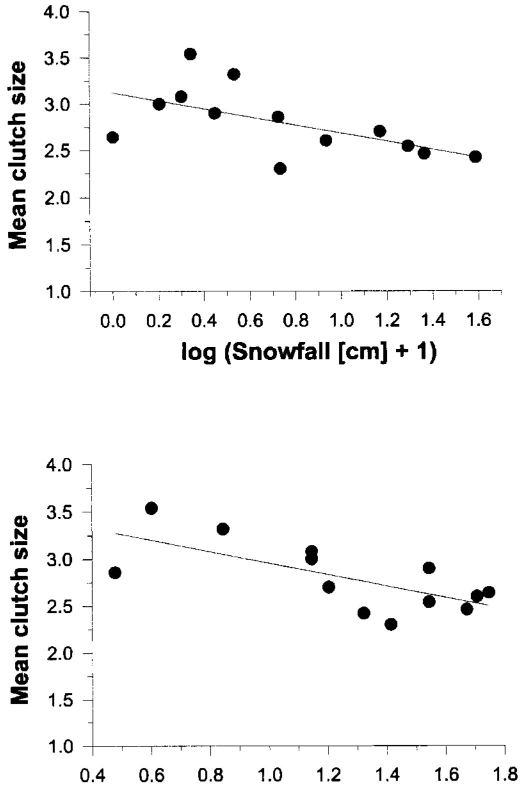

FIG. 2. Relationship between clutch size and annual snowfall (upper) and total rainfall (lower) during the prelaying period. Linear regression: clutch size = 3.12 − 0.44 log (snowfall + 1); $r = 0.60$, $P = 0.03$. Linear regression: clutch size = 3.57 − 0.61 log (h of rain); $r = 0.69$, $P = 0.01$.

mortality, we recalculated weather parameters using only data recorded during storms (i.e. three or more days of consecutive rainfall). Precipitation and chick mortality were significantly positively correlated (Fig. 3).

Breeding phenology also played a part in the relationship between weather and chick mortality. Severe storms were common on the study area from mid-August onwards. Chicks usually had reached the age of thermoregulation by the time the storms arrived, but the spring blizzard of 1987 was associated with a 10-day delay in laying. This delay meant that a storm hit the study area when the mean chick age was less than 21 days (the approximate age of thermoregulation [Enderson et al. 1972, Hovis et al. 1985]) and was coincident with high chick mortality.

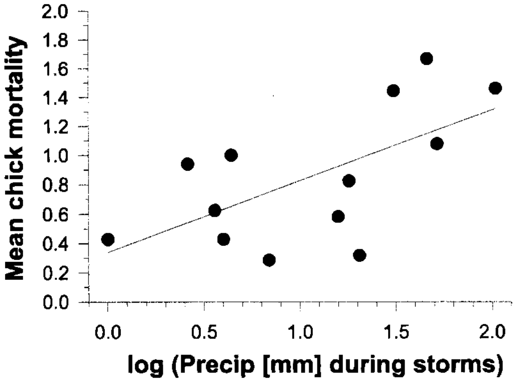

FIG. 3. Relationship between chick mortalilty and annual precipitation during storms. Linear regression: mean chick mortality = 0.34 + 0.49 log (precipitation during storms); $r = 0.63$, $P = 0.02$. A storm was defined as three or more days of consecutive rainfall.

Over the entire study period, 18% of the territorial pairs failed to lay eggs (57 of 309), 22% of the pairs that laid eggs failed during incubation (55 of 252), and 15% of the pairs that hatched young failed during the nestling stage (29 of 197). There was no significant difference in failure rates among the three stages of the breeding season ($\chi^2 = 3.69$, df = 2, $P = 0.16$).

Discussion.—Peregrine Falcons at Rankin Inlet had a narrow range of laying dates (annual mean of 12 days) compared with those nesting at tropical and temperate latitudes (39 days in Scotland [Mearns and Newton 1988]; 45 days in Australia [Olsen and Olsen 1989a]; three to seven months in Africa [Mendelsohn 1988, Thomsett 1988]). The Scottish, Australian, and African populations are nonmigratory. Migratory peregrines from other northern areas also have a narrow range of laying dates: 21 days in Alaska (Cade 1960), 18 days in the central Canadian arctic (Poole and Bromley 1988), and 30 days in southern Greenland (Falk et al. 1986). We suggest that the constraints of August weather and the impending migration result in the narrow range of laying dates in peregrines breeding at high latitudes. Factors other than weather must be responsible for the precise timing of laying, however, because weather was only important at Rankin Inlet as a proximate modifier of breeding phenology in 1 of 13 years.

We found no relationship between weather and the number of pairs establishing territories, suggesting that the size of the breeding population is regulated by other factors. Production of young varied widely. Mean brood size at fledging varied from 0.6 to 2.5 young per pair, a four-fold difference. In comparison, mean brood size of peregrines differed by a factor of 1.7 in Australia (Olsen and Olsen 1989b) and 2.4 in Scotland (Mearns and Newton 1988).

The higher variation in production in our population could be due in part to differences in data collection. Because other researchers find most of the territorial pairs after egg laying (or later), they may have missed pairs that failed early. Conversely, the other populations are nonmigratory, so failed pairs may be easy to find. In any case, if we eliminate nonlaying pairs from our data set, then annual variation in production at Rankin Inlet still was higher than in the Scottish or Australian populations. We suggest that the greater variation in productivity in our study area is due to two factors: weather and food supply. At Rankin Inlet, years of low production were coincident with bad weather. The food supply/production hypothesis (Court et al 1988a) is speculative and stems from the observation of a single year of extremely high production (mean brood size of 2.5 during a year with no severe weather events) that coincided with a peak in microtine rodent density (microtines are an important food of Rankin Inlet peregrines; Bradley and Oliphant 1991).

Relationships between clutch size and weather like we documented for Rankin Inlet (Fig. 2) have been reported for other birds (Newton 1986, Nias and Ford 1992) but not for peregrines. Newton (1979, 1986) suggested that clutch size in raptors is determined primarily by food supply to the female during egg formation. We did not measure prey abundance or hunting success, but severe weather effects are not contradictory to Newton's hypothesis. Inclement weather can increase the energetic costs of thermoregulation (i.e. a direct effect; Whyte and Bolen 1984, Tatner 1990, Castro et al. 1992) and can hinder the male's ability to feed the female (i.e. indirect effects) by reducing the efficiency of aerial hunting (White 1975, Ratcliffe 1980, Rijnsdorp et al. 1981, Milsom 1987, Machmer and Ydenberg 1989, Olsen and Olsen 1992) or by reducing the availability of prey (Jehl and Hussel 1966, Pullainen 1978, Ojanen 1979, Hendricks and Norment 1992). Therefore, severe weather may be a corollary to the food-supply hypothesis. Our data do not allow us to differentiate between direct and indirect effects.

Weather affected egg mortality in only one year, 1986. Because 1986 had the sixth highest June snowfall in the last 30 years, the peregrines probably experience such an event about once every 5 years. In contrast to the catastrophic egg mortality at Rankin Inlet, there was a linear relationship between breeding success (proportion of clutches resulting in fledged young) and weather during hatching for peregrines in Scotland (Mearns and Newton 1988) and Australia (Olsen and Olsen 1989b).

We found a linear relationship between chick mortality and precipitation during lengthy storms. Apparently, severe weather could be survived as long as it was broken up by spells of good weather. Chick mortality of peregrines in Scotland and Australia, however, did not vary with weather (Mearns and Newton 1988, Olsen and Olsen 1989b). In this respect, at least two factors distinguish Rankin Inlet from Scotland and Australia: Rankin Inlet often has storms during the nestling period, and the window for successful breeding is very brief.

Failure rates were similar among the three stages of the breeding season. We reanalyzed Mearns and Newton's (1988) data from Scotland and found that failure rates were higher during the nestling stage (29%) than during the prelaying (17%) and incubation (19%) stages ($\chi^2 = 13.5$ df = 2, $P < 0.01$). Mearns and Newton reported that most of their chick mortality occurred within a day or two of hatching and was correlated with rainfall during May, which included the hatching period. Thus, the influence of weather on reproductive success was similar throughout the breeding season at Rankin Inlet, but apparently was restricted to a short period (i.e. around the time of hatching) in Scotland.

Conclusions.—Our data were derived from peregrines that breed in a climate that is harsher and less predictable than that experienced by other populations for which data are available. In many ways, the breeding ecology of peregrines at Rankin Inlet (i.e. short breeding season, importance of breeding early, variable reproductive output) more closely resembles that of other species breeding at northern latitudes (Jehl and Hussel 1966, Reeves et al. 1976, Pullainen 1978, Ely and Raveling 1984, Hendricks and Norment 1992) than of peregrines breeding in more benign climates. The high variability in breeding success at Rankin Inlet was strongly associated with weather, but weather was not the only important influence on breeding success. Also, breeding success was quite high for the species (cf. Cade 1960, Hickey 1969, Moore 1987, Cade et al. 1988, Mearns and Newton 1988, Olsen and Olsen 1989b), so there must have been compelling ecological reasons (e.g. food availability) for peregrines to brave the severe weather of the region.

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