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DAY-TO-DAY VARIATION IN NEST ATTENTIVENESS OF WHITE-RUMPED SANDPIPERS[1]

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Abstract. We studied the nest attentiveness of six female White-rumped Sandpipers (*Calidris fuscicollis*), a species with uniparental care which incubates in the continuous daylight of the arctic summer. We used correlation and multiple regression analyses to determine how well day-to-day variation in recess time/day, number of trips/day, and average trip length/day could be explained by date, concurrent weather, behavior on the previous day, and weather on the previous day. Both previous and concurrent weather were important predictors of incubation behavior, while date and previous behavior were not. We therefore conclude that incubation behavior on a given day is not simply a function of current conditions. Behavior appears at least to integrate the effects of both present weather and weather on the previous day.

Key words: Calidris fuscicollis; *incubation behavior; nest attentiveness; past behavior; past weather; sandpiper; uniparental care; weather.*

INTRODUCTION

Weather should have an important effect on the nest-departing decisions of incubating birds because it influences the cooling rates of eggs and the metabolic rates and foraging success of adults. By influencing the cooling rates of eggs (Drent 1970), weather affects both embryo metabolism (Lundy 1969, Norton 1970, Romanoff and Romanoff 1972) and the adult energy costs in keeping eggs warm or rewarming cold eggs (El-Wailly 1966, Mertens 1980, Biebach 1984). Adult metabolic rates are affected by ambient temperatures below the thermoneutral zone (Norton 1973, Ricklefs 1974), by solar radiation when ambient temperatures are low (de Jong 1976), by wind speed through convective heat loss (Goldstein 1983), and by relative humidity through convective heat loss (Kendeigh 1934). Finally, weather can affect a bird's energy budget by altering food abundance and, therefore, foraging success (Pienkowski 1983, Bryant and Westerterp 1983).

The decisions that incubating birds make to keep their eggs warm in the face of changing weather can profitably be considered at two levels. First, they can structure their daily activities to maximize the difference between costs and benefits with respect to the diel cycle of weather (Daan 1981). Since many weather variables follow a more or less predictable cycle each day, incubating birds may profitably adjust their nest attentiveness to minimize egg-cooling as weather conditions change. To do this the nest attentiveness itself can follow a diel cycle modified slightly by concurrent weather conditions (Cartar and Montgomerie 1985). Second, incubating birds can respond to day-to-day changes in the weather, though these may be less predictable. For example, nest attentiveness may change through the incubation period as the general weather conditions and the needs of the developing embryos change. On a finer time scale, the overall nest attentiveness on a given day may also be influenced by the previous day's activities (and weather), influencing the needs of the incubating parent on a given day.

Most studies of incubation attentiveness have focused on how birds structure their within-day activities with respect to the cyclic aspects of weather (e.g., Kendeigh 1952, Haftorn 1978). We know surprisingly little about day-to-day variation in behavior and whether within-day responses are sufficient in themselves to explain any among-day differences. Thus three patterns of day-to-day variation in attentiveness might be expected. First, incubating birds might adjust their attentiveness schedules only in response to concurrent weather. In this case within-day responses to weather would be sufficient to explain any among-day patterns. Second, incubators

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could respond to both weather and the changing embryo requirements such that both within-day weather and stage of incubation would be the best predictors of attentiveness. Third, incubators could adjust their attentiveness in response to concurrent weather and their own needs. In this case we would expect either the past behavior of the incubating parent or past weather to influence its activities. For example, if a parent remained on its nest during a particularly cold day to keep the eggs from freezing, we might expect it to spend more time off the nest the following day than would be expected from concurrent weather alone, simply to replenish its own metabolic reserves.

In this paper we analyze day-to-day variation in the incubation behavior of an arctic-nesting uniparental incubator: the female White-rumped Sandpiper (*Calidris fuscicollis*). Given the low ambient temperatures during the incubation period, the small female body size (about 44 g), and the poorly insulated nest, White-rumped Sandpiper incubation is a good system for study of the incubation strategies of birds nesting in extreme environments. Here we assume that White-rumped Sandpipers regulated the temperatures of their eggs within tolerable limits (see Cartar and Montgomerie 1985), and we focus on the correlations between the nest attendance schedules and current weather, previous weather, previous behavior, and date.

METHODS

This study was completed during the summer of 1982 at Sarcpa Lake, on the Melville Peninsula, NWT, Canada (68°33′N, 83°19′W, altitude 250 m; see Montgomerie et al. 1983). Nests 2, 3, 5, and 7 were found during the laying stage, and nest 1 in the first two days of incubation. Clutches were completed between 20 and 29 June and all but one nest (nest 1) were preyed on by an arctic fox (*Alopex lagopus*) within eight days of hatching. Bird numbers used in this paper correspond to those of Cartar and Montgomerie (1985).

In 1982 female White-rumped Sandpipers arrived at our study site during the second week of June, and all of the four-egg clutches were complete by 29 June (median 25 June, $n = 6$). The incubation period in this species averages about 21 days (Parmelee et al. 1968, pers. observ. 1981). At Sarcpa Lake females nested on solifluction slopes and, less often, in wet meadows at nest densities up to four nests/km^2. Females spent on average 17.5% of their time off the nest in 1982. Typically an off-nest trip consisted of flying 50 to 300 m to a feeding area, feeding rapidly, and flying back to the nest (average trip length was 10.5 min).

We monitored nests with Minolta XL-401 Super-8 movie cameras equipped with intervalometers, placed about 2 m from the nest. One frame was exposed every minute in these cameras. Filming began after the last egg was laid and because of the continuous daylight, birds were photographed on their nests at all hours of the day. Weather was recorded at a central station no more than 2.3 km from any nest studied. Temperature, solar radiation, and wind speed were measured with a CR21 micrologger (Campbell Scientific Inc.) equipped with a model 101 temperature probe, a Met-one® 014A wind speed sensor (a three-cup anemometer), and a LI-COR® LI-200S pyranometer sensor. The wind speed and solar radiation sensors were mounted 2.0 m above ground on a tripod. The temperature probe was housed in a Stevenson screen 0.7 m above the tundra. Barometric pressure and relative humidity were recorded with a HI-Q model 5010 meterograph (a spring-wound chart recorder with a one-day drum rotation) housed in the Stevenson screen. Rain was uncommon, occurring only infrequently on 9 to 11 July, and is therefore not formally considered here. Birds did, however, spend more time on their nests during rain (Cartar 1983).

ANALYSIS

We analyzed three variables of White-rumped Sandpiper incubation scheduling: the total time spent off the nest each day (i.e., recess time/day), the average length of an off-nest trip for each day (i.e., mean trip length), and the total number of trips made each day (i.e., trips/day). Recess time/day indicates both the amount of time the female spent feeding and the length of time that embryos were exposed to the environment on a given day, and is the product of mean trip length and trips/day. We analyzed trips/day and mean trip length to determine how the observed recess time/day was accomplished, and to determine how these two components were themselves influenced by both current and previous weather, and by behavior and date.

To examine how nest attendance was influenced by day-to-day differences in weather, we calculated correlations between the daily mean

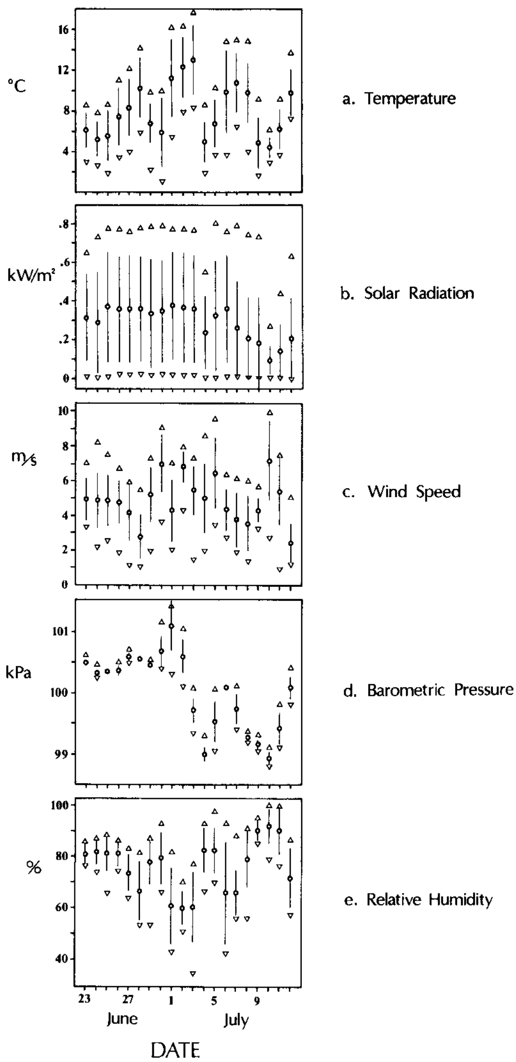

FIGURE 1. Seasonal trends in weather. Data are based on hourly samples. Circles with vertical bars show the mean ± 1 SD. Open triangles show maximum and minimum values.

of each weather variable and each bird's total recess time/day, trips/day, and mean trip length/day. We analyzed each bird separately, as one-way analysis of variance showed significant among-bird differences in each of the three behavioral variables. To examine which variables were best predictors of nest attentiveness of each female, we performed stepwise multiple regressions, using the maximum R^2 improvement model, since this model is less sensitive to the order in which variables are added (SAS Inst. 1982). Stepwise regressions were used to select subsets of variables. Our intent in using the stepwise approach was to to identify key independent variables, to infer which of these exerted the greatest effects on bird behavior. More convincing would be the simultaneous comparisons of all variables resulting from direct multiple regression, but ruled out by our small sample sizes and large number of independent variables. Regression analyses contrasted trips/day, mean trip length, and recess time/day as dependent variables with Julian date (as a measure of stage of incubation), weather variables on that day and on the previous day, and that incubation behavior for the previous day as independent variables.

RESULTS

WEATHER

During the 1982 incubation period at Sarcpa Lake, the temperatures recorded at Hall Beach, 75 km to the NE, averaged 1.3°C warmer than normal (based on a 1941 to 1970 average, Environment Canada 1982). Since there was a significant correlation ($r = 0.66$, $P < 0.01$) between temperatures at Hall Beach and Sarcpa Lake during the study period, we assume that the 1982 incubation period at Sarcpa Lake was slightly warmer than average.

Weather during White-rumped Sandpiper incubation varied considerably (Fig. 1). Average conditions during the period in which incubation behavior was studied (23 June to 13 July) were: temperature, 7.95°C; solar radiation, 0.289 kW/m²; wind speed, 4.85 m/s; barometric pressure, 100.2 kPa; and relative humidity, 76.1%. Several pairs of weather variables were significantly correlated (Table 1), but are considered separately since each could potentially influence behavior in a unique manner (Cartar and Montgomerie 1985).

FACTORS AFFECTING INCUBATION BEHAVIOR

Previous day's behavior. Nest attentiveness on the previous day had little effect on White-rumped Sandpiper incubation schedules. Recess time/day was not significantly correlated with that of the previous day for any bird (Table 2). For two birds trips/day were significantly and positively correlated on consecutive days (Table 3). For one of these two birds (female 2), however, trips/day from the previous day did not significantly enter the regression model including all variables, sug-

TABLE 1. Pearson product-moment correlations between weather variables, based on daily averages of hourly averages (24 June to 12 July, $n = 19$). (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.)

	Radiation	Windspeed	Pressure	Humidity
Temperature	0.570*	−0.305	0.442	−0.925***
Solar radiation		0.042	0.765***	−0.700**
Wind speed			−0.067	0.284
Barometric pressure				−0.595**

gesting that the correlation was spurious. Mean trip length was also positively correlated with the previous day's trip length for two females (Table 4), but neither of these entered significantly into the regression model, suggesting again that the correlation was spurious.

Seasonal effects. Seasonal trends in recess time/day were not pronounced (Fig. 2), and were only significant for two birds, and in opposite directions (see date, Table 2). The last few days of incubation were not observed for five of the nests, so conclusions of these analyses may not extend to this final period. This aside, date made no significant contribution to any stepwise regression for any bird. Overall, there was a tendency for birds to make more off-nest trips as incubation progressed (Fig. 3; four birds significantly increased the trips/day and for one of these birds trips/day entered significantly into the regression model [Table 3]). Female 5, however, significantly decreased her number of trips through the season, but this relation was not significant in the regression model (Table 3). Mean trip lengths decreased as incubation progressed (Fig. 4), as might be expected since there was little change in recess time/day and an increasing trend in

TABLE 2. Relationships between recess time/day and current weather, previous day's weather, and previous day's behavior. Spearman's rank correlations are shown for each bird. Bracketed numbers are standardized regression coefficients for significant ($P < 0.05$) variables as selected by stepwise multiple regressions, using the maximum R^2 selection criterion. (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.)

	Female					
Variable	1	2	3	5	7	8
(1) Nonweather factors						
Recess time in previous day	−0.24	0.40	0.19	0.42	−0.23	0.01
Date	−0.08	0.52*	0.32	−0.59*	0.06	−0.01
(2) Concurrent weather						
Temperature	0.25	0.14	−0.05	0.67** (0.72)	−0.17 (−0.46)	0.15
Solar radiation	0.12	−0.23	−0.33	0.72**	−0.07	0.09
Wind speed	−0.53*	−0.31 (−0.50)	−0.14	−0.15	0.30	−0.05
Barometric pressure	0.03	−0.39 (−0.50)	−0.58* (−0.80)	0.44	−0.31	0.05 (−0.50)
Relative humidity	−0.21	−0.02	0.16	−0.71**	0.07	0.01
(3) Previous day's weather						
Temperature	0.21	−0.05	0.04	0.47	0.50 (0.73)	−0.04
Solar radiation	0.19	−0.17	0.03 (0.47)	0.65**	0.33	0.13
Wind speed	0.23	0.52* (0.54)	0.41 (0.48)	0.21	−0.01	0.79** (0.84)
Barometric pressure	0.21	−0.44	−0.38	0.60*	−0.01	−0.21
Relative humidity	−0.28	0.15	0.05	−0.41	−0.40	−0.04
Variation explained by regression	ns	66%	65%	53%	66%	64%
Sample size	17	15	17	14	11	11

TABLE 3. Relationships between number of trips/day and current weather, previous day's weather, and previous day's behavior. Spearman's rank correlations are shown for each bird. Bracketed numbers are standardized regression coefficients for significant ($P < 0.05$) variables as selected by stepwise multiple regressions, using the maximum R^2 selection criterion. (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.) Sample sizes as in Table 2.

	Female					
Variable	1	2	3	5	7	8
(1) Nonweather factors						
Number of trips in previous day	0.30	0.68**	0.38	0.64** (0.48)	0.11	0.16
Date	0.64***	0.78*** (0.77)	0.47*	−0.80***	0.48* (1.00)	0.39
(2) Concurrent weather						
Temperature	−0.24	−0.07	−0.07	0.57* (0.60)	0.25	0.16
Solar radiation	−0.62**	−0.59*	−0.43	0.83***	−0.06	−0.07
Wind speed	0.03	−0.43 (−0.37)	−0.15	−0.02	−0.07	−0.33
Barometric pressure	−0.68** (−0.68)	−0.45	−0.65** (−0.59)	0.64**	−0.13	−0.06
Relative humidity	0.43	0.22	0.23	−0.71**	−0.11	0.04 (−1.28)
(3) Previous day's weather						
Temperature	−0.13	−0.33	−0.03	0.45	−0.39 (−2.08)	−0.14
Solar radiation	−0.42	−0.65**	−0.18	0.66**	−0.24	−0.16
Wind speed	0.27	−0.00	0.17	0.05	0.26 (0.15)	0.38
Barometric pressure	−0.56*	−0.64**	−0.46*	0.79***	−0.29	−0.44 (−1.50)
Relative humidity	0.12	0.51	0.11	−0.45	0.36 (−1.88)	0.24
Variation explained by regression	44%	84%	39%	64%	93%	78%

trips/day. All but female 5 made shorter trips as incubation progressed and three of these were significant (Table 4) suggesting that the seasonal trend may have been due to changing weather rather than a change in the embryo's requirements.

Concurrent weather. There was considerable variability among females in the apparent effects of each weather variable on the three measures of incubation attentiveness (Tables 2, 3, 4). In general, though, females tended to spend more time off their nests when egg-cooling would be minimized. For example, females spent more time off their nests per trip when temperature and solar radiation were highest (positive correlations, Table 4) and when wind speed and relative humidity were lowest (negative correlations, Table 4). There was also a tendency toward positive correlations between trip length and barometric pressure, indicating that the birds spent more time off their nests when the weather was warm, sunny, and dry.

Stepwise regressions showed that three of the weather variables—temperature, wind speed, and, especially, barometric pressure—were important predictors of recess time/day (Table 2). For five of the six birds, at least one weather variable significantly predicted recess time/day (Table 2), trips/day (Table 3), and mean trip length (Table 4).

Previous day's weather. Weather conditions on the previous day importantly predicted recess time/day for several birds (Table 2). The regression analyses show that three birds spent signif-

TABLE 4. Relationships between average trip length/day and current weather, previous day's weather, and previous day's behavior. Spearman's rank correlations are shown for each bird. Bracketed numbers are standardized regression coefficients for significant ($P < 0.05$) variables as selected by stepwise multiple regressions, using the maximum R^2 selection criterion. (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.) Sample sizes as in Table 2.

Variable	Female 1	Female 2	Female 3	Female 5	Female 7	Female 8
(1) Nonweather factors						
Avg. trip length in previous day	0.61**	0.68**	0.10	0.51	0.18	0.21
Date	−0.77***	−0.66**	−0.15	0.46	−0.69*	−0.48
(2) Concurrent weather						
Temperature	0.48*	0.56*	0.17	0.03	0.06	0.34 (0.54)
Solar radiation	0.70**	0.91*** (0.88)	0.26	−0.30	0.53	0.38
Wind speed	−0.36 (−0.46)	0.33	−0.06	−0.43 (−0.68)	0.20	0.57* (0.66)
Barometric pressure	0.77***	0.64**	0.38	−0.35	0.61* (0.55)	0.30
Relative humidity	−0.56*	−0.66**	−0.32	0.15	−0.22 (0.99)	−0.39
(3) Previous day's weather						
Temperature	0.14 (−0.32)	0.15	0.18	−0.25 (−1.65)	0.06	0.15
Solar radiation	0.63**	0.59*	0.38 (0.49)	−0.30	0.45 (0.95)	0.40
Wind speed	−0.06	0.31	0.16	0.21	0.44	−0.06
Barometric pressure	0.76*** (0.93)	0.65**	0.25	−0.56* (−0.95)	0.39	0.62*
Relative humidity	−0.29	−0.33	−0.16	0.30 (−1.74)	−0.13	−0.29
Variation explained by regression	94%	82%	24%	87%	96%	72%

icantly more time off their nests if the wind was strong on the previous day. Note, however, that birds tended to spend more time on their nests if concurrent wind speed was high (Table 2).

The relationships between previous weather and trips/day (Table 3) and mean trip length (Table 4) were less clear. The regression analyses show that trips/day of only two females were significantly dependent on previous weather (Table 3). Weather from the previous day significantly predicted the trip lengths of four birds (Table 4).

DISCUSSION

This study supports the idea (e.g., Webb and King 1983) that incubation behavior can be influenced by either weather or behavior on the preceding day. These "historical factors" probably manifested themselves by effecting changes in the birds' metabolic reserves, which can serve as a physiological "memory" of past circumstances.

When faced with the increased metabolic costs of incubating during a cold day, a female White-rumped Sandpiper could either forage more and maintain body condition, or incubate more and suffer depleted metabolic reserves. If the incubating birds were not relying on stored reserves during cold weather their daily nest attentiveness should have decreased in cold conditions (i.e., low temperature, dark, high wind speed, high humidity). Alternatively, if the birds relied on stored metabolic reserves on colder days, attentiveness should have increased during these days.

It appears that the metabolic stresses imposed by weather on a given day exerted some significant effects on incubation behavior on the following day. Thus these birds may have depleted

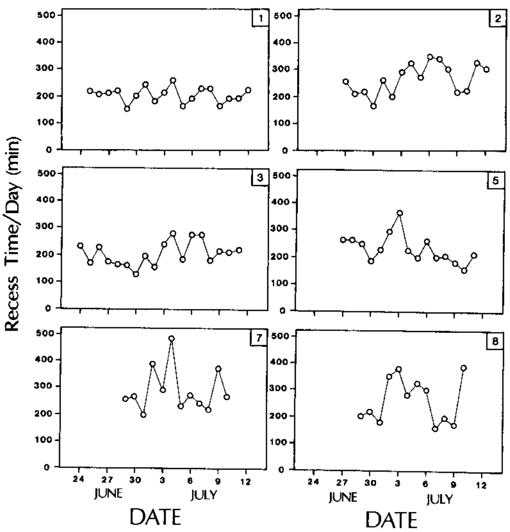

FIGURE 2. Seasonal trends in recess time/day.

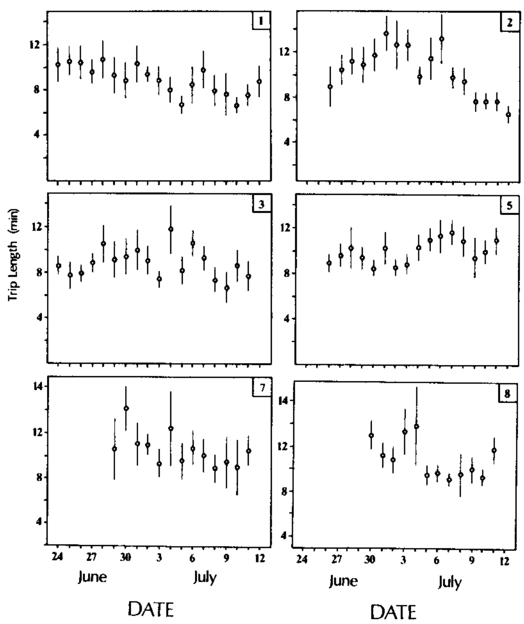

FIGURE 4. Seasonal trends in average trip length/day. Female number appears in the upper right corner of each graph. Means and 95% confidence intervals are shown. Sample sizes for each mean ranged from 10 to 48 trips, averaging 25.5 (SD = 8.7).

and replenished metabolic reserves in the short-term (one day to the next). To critically test this, though, evidence is needed on the relationship between body mass and immediate daily weather conditions.

Because embryos are progressively less tolerant of cold temperatures as they develop (MacMullan and Eberhardt 1953, Romanoff and Romanoff 1972, Batt and Cornwell 1972), weather during the last few days of incubation may have the most critical effect on embryo survival. A moderating influence here is that older embryos also cool less rapidly because they have some thermoregulatory ability (Drent 1970). Since well-developed embryos cool slowly, but die easily when cold, the seasonal trend of increasing the number of trips and decreasing trip lengths (Figs. 3 and 4) is consistent with the notion that females capitalize on this cooling phenomenon to regulate the temperatures of well-developed embryos within optimal limits. An old embryo can thermoregulate during short trips, but not during long ones. More frequent off-nest trips, however, may serve to attract predator attention to the nest (Erckmann 1981), and may be an important factor in keeping trip frequency in check.

In scheduling their within-day activities with respect to weather, female White-rumped Sandpipers primarily adjusted the number of trips that they made, not their average trip length (Cartar and Montgomerie 1985). However, this tendency did not carry through to the daily level: weather and previous behavior explained variation in average trip length and number of trips almost equally well (an average of 76% and 67%,

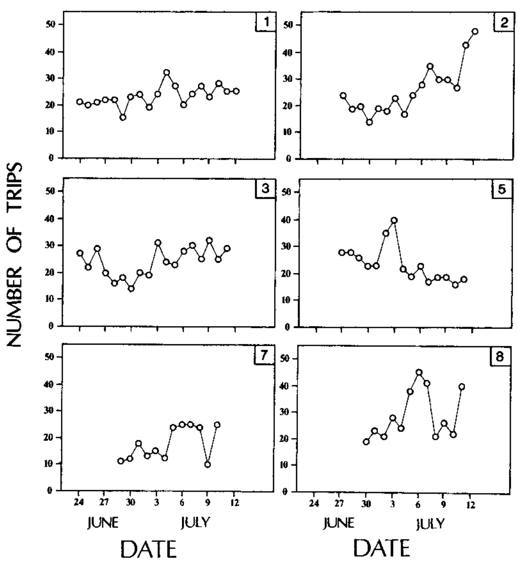

FIGURE 3. Seasonal trends in number of trips/day.

respectively; averaged from Tables 3 and 4). This suggests that birds made decisions at two independent temporal levels: within- and among-day.

As shown by the regressions, there were sizable among-bird differences in response to individual weather variables, some of which may have resulted from using a stepwise model (but note that similar patterns exist in the correlation structure, Tables 2 to 4). Despite this, there was a surprising consistency in the overall variation explained in recess time/day for each bird (except for female 1) when all factors were considered (Table 2). This variability suggests that although the factors considered in this study were important (explaining roughly ⅔ of the variation in behavior), they were not so influential as to affect attendance schedules of different birds in the same way. Among-female differences may result from individual differences in body condition, nest microclimate, or experience, but can still lead to an overall pattern that is consistent among birds with respect to thermal conditions, but not with respect to each individual weather variable. For example, if birds make off-nest trips in the thermally optimal conditions, they can do so more on warm, and/or sunny, and/or calm, and/or dry days. The birds in this study appeared not to share the same attitude towards these different thermal factors. Hence, a simple-minded consideration of temperature alone would have rejected thermal factors as being important, while consideration of several weather factors suggests that thermal conditions were very important.

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