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Geographical Trends in Clutch Size: A Range-wide Relationship with Laying Date in American Pipits

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Many species of terrestrial birds produce larger clutches at higher latitudes within their breeding ranges. This pattern has been explained as a response to increased day length (Lack 1954, Hussell 1985), increased seasonality of food resources (Ricklefs 1980), or decreased climatic stability (Cody 1966) as one moves from equatorial to polar regions. In each case the outcome is an increased availability of food that can be delivered to dependent offspring, thus allowing for larger clutches and broods. Several modifications and refinements of these hypotheses have been advanced (e.g. Skutch 1967, Murray 1979, Slagsvold 1981), and the topic remains an active area of investigation.

The relationship between laying date and clutch size is another pattern that has been widely documented in birds. Earlier laying within a season typically results in larger clutches (Lack 1954, Perrins

1970), and mean clutch size increases during years of early nesting (Järvinen 1989a, Perrins and McCleery 1989). Few studies of single species, however, have examined a number of populations over a large range of latitudes to see if latitudinal patterns in mean clutch size relate in some predictable way to annual variation in mean laying date within populations.

Here, I present evidence that annual mean clutch size of American Pipits (*Anthus rubescens*) is strongly correlated with the annual mean date of clutch initiation for each population, and that latitudinal differences in day length, seasonality of food, and climatic instability need not be invoked to explain the larger average clutch size at higher latitudes shown by this species. A corollary resulting from this observation is that egg laying begins earlier (on average) at higher latitudes for American Pipits, a pattern counter to the normal expectation for most species.

Study areas and methods.—American Pipits breed in treeless tundra habitats in North America and eastern Siberia. They occupy high-elevation alpine areas

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from Arizona and New Mexico through western Canada and maritime and arctic tundra at lower elevations from Siberia and Alaska to the Canadian High Arctic and western Greenland. The climate throughout the breeding range is harsh and variable and is characterized by relatively low ambient temperatures, frequent strong winds, and periodic rain and snow storms. The nesting season is compressed; egg laying typically occurs over a 45-day period from late May to mid-July. Pipits are single-brooded but will renest if the first clutches are destroyed early in the breeding season (Hendricks 1991). Eggs are laid daily, incubation lasts about 14 days (usually beginning with the last egg), and the young remain in the nest for an additional 14 days. A more complete account of pipit life history is available in Verbeek and Hendricks (1994).

To examine latitudinal trends in clutch size, I obtained data from throughout the breeding range of American Pipits (Verbeek and Hendricks 1994: appendix 2); the mean latitude of these sample localities ranged from 36 to 64°N. Sample localities were geopolitical areas (usually states or provinces) where cumulative sample size of clutches was five or greater (n = 14 localities). I chose this arbitrary sample size to increase confidence in average clutch-size values while maintaining enough sites for a meaningful analysis.

Information on pipit clutch size and laying date for local populations was obtained from 1987 to 1989 at Beartooth Pass (3,200 m elevation) and Chain Lakes (2,900 m) in the Beartooth Mountains, Park County, Wyoming (45°00'N, 109°30'W). Beartooth Pass is near the summit of the Beartooth Plateau, one of several large alpine plateaus (some more than 200 km²) exceeding 3,000 m elevation near the Montana-Wyoming border. The Chain Lakes site is near treeline in a series of large subalpine meadows. Two additional years of data (1963 and 1964) from Beartooth Pass were available in Verbeek (1970).

Few population-level studies report clutch sizes of American Pipits, and sample sizes tend to be small. To maintain reliable estimates of clutch size and laying date while increasing my sample of years, I restricted analyses to studies that reported clutch sizes for at least nine nests for single years and study areas. Variances of sample clutch-size means did not differ (F_{max} test, $P > 0.1$), indicating that the smaller samples tended to be as representative as samples of ≥30 clutches. Sources for data from other localities were Miller (1988, pers. comm.) for California (36°30'N, 118°30'W; Mitre Basin, Tulare County; 3,600 m elevation); the Cornell North American Nest Records Card Program for Colorado (40°40'N, 105°40'W; Rocky Mountain National Park, Larimer County; 3,600 m); Sutton and Parmelee (1954) for the Northwest Territories (63°40'N, 68°30'W; Frobisher Bay, Baffin Island; <300 m); and the Alaska Nest Rec-

ords Scheme for Alaska (65°30'N, 145°20'W; Eagle Summit, ca. 150 km NE of Fairbanks; 1,000 m).

Clutches or broods of fewer than three eggs and/or young were excluded from analyses because there are no confirmed complete clutches of 1 or 2 eggs for American Pipits (Verbeek and Hendricks 1994); otherwise, the maximum number of eggs and/or young was considered to be the complete clutch size. Where only one nest check was made (the case for many of the nest record cards from Alaska and Colorado, and some of the data from Baffin Island), I estimated laying date by assuming that the nest, when found, was at the mid-point day of that phase of the nesting cycle (i.e. day 7 of incubation or posthatching) and then backdating to when the first egg was laid, unless there was evidence that indicated a different date of laying (e.g. a comment stating that young were naked or had their eyes closed).

Statistical analyses followed standard procedures (Sokal and Rohlf 1981), with statistical significance assumed when $P < 0.05$. I treated samples from single populations but different years, and single years but different populations, as equally independent. Technically they are not, but violation of this assumption is unavoidable to show the pattern I identify regarding the significance of laying date *each year* at every site. There is significant variation in both clutch size and laying date within sites among years, which should counteract any site effects. Furthermore, the correlation between laying date and clutch size within the Wyoming populations (see Results) closely resembles the pattern among populations, supporting the generality of the results.

Results.—Mean clutch size increased significantly with latitude (r = 0.676, n = 14, $P < 0.01$) for cumulative state and province samples across the breeding range of the American Pipit (see Verbeek and Hendricks 1994). Cumulative mean clutch size also varied significantly (one-way ANOVA, F = 6.91, df = 5 and 370, $P < 0.001$) among the smaller sample of local populations (Table 1: site totals). Significant pairwise differences (Bonferroni multiple comparisons tests) were present between high- and mid-latitude sites, such as Eagle Summit, Alaska versus Rocky Mountain National Park, Colorado ($P < 0.001$) or Wyoming ($P < 0.001$ and $P = 0.003$ for Beartooth Pass and Chain Lakes, respectively), with larger mean clutch sizes at the high-latitude site. Mean clutch size at Frobisher Bay, Baffin Island at 63°N, however, was smaller than at Mitre Basin, California at 36°N (Table 1), showing that anomalies exist within the general pattern of larger clutches at high latitudes.

Differences in clutch size between populations at similar latitudes approached statistical significance (e.g. Alaska vs. Baffin Island, $P = 0.071$; California vs. Colorado, $P = 0.080$). Smaller sample sizes may have inflated P-values for the within-latitude comparisons, but the results indicate that something oth-

TABLE 1.   Annual clutch size ($\bar{x} \pm$ SD, *n* in parentheses) of American Pipits from six sites in North America.

Year	California (36°N)	Colorado (40°N)	Wyoming (45°N)[a]	Wyoming (45°N)[b]	Baffin Island (63°N)	Alaska (65°N)
1953					4.9 ± 1.0 (13)	
1963			4.6 ± 0.7 (37)			
1964			4.8 ± 0.7 (50)			5.7 ± 0.5 (12)
1966						5.6 ± 0.9 (9)
1967		4.3 ± 1.2 (17)				5.8 ± 0.7 (14)
1968		4.8 ± 0.8 (13)				
1983	4.8 ± 0.8 (9)					
1985	5.4 ± 0.8 (15)					
1987			5.5 ± 0.6 (30)	5.4 ± 0.7 (20)		
1988			5.2 ± 0.9 (46)	5.0 ± 0.8 (17)		
1989			5.0 ± 0.8 (53)	4.7 ± 0.8 (21)		
Total	5.2 ± 0.9 (24)	4.5 ± 1.0 (30)	5.0 ± 0.8 (216)	5.0 ± 0.8 (58)	4.9 ± 1.0 (13)	5.7 ± 0.7 (35)

[a] Beartooth Pass (3,200 m elevation).
[b] Chain Lakes (2,900 m elevation).

er than day length is affecting clutch size. Mean clutch size in California was larger than in Colorado even though the California site was farther south. Although clutch size in Alaska, the most northern site, was larger than on Baffin Island, the difference (0.8 eggs) between the two sites was large for only 2° of latitude. In both comparisons, the differences appear anomalous and require explanation.

Mean clutch size also varied significantly at single sites (Table 1). Means for five years at Beartooth Pass, Wyoming ranged from 4.6 to 5.5 ($F = 7.81$, df = 4 and 211, $P < 0.001$); for three years at Chain Lakes, also in the Beartooth Mountains of Wyoming, clutch size ranged from 4.7 to 5.4 ($F = 4.82$, df = 2 and 55, $P = 0.012$). At Beartooth Pass alone, the range in mean clutch size for five years spanned 60% of the
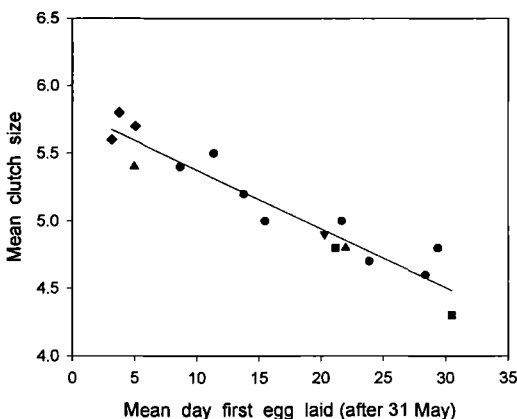

FIG. 1.   The relationship between annual mean clutch size of American Pipits and annual mean laying date. Points are values for single years: diamonds, Alaska; triangles, California; squares, Colorado; circles, Wyoming; inverted triangle, Baffin Island.

annual variation in means for all sites combined (Table 1), and virtually 100% of the latitudinal variation in cumulative mean clutch size (i.e. the mean for all clutches at a given latitude; see appendix 2 in Verbeek and Hendricks 1994) across the entire breeding range. This suggests that annual mean clutch size of American Pipits at a given site could be identical to the cumulative mean at any latitude.

The available population samples indicated that there were significant differences among sites in the average onset of egg laying. For example, 10 of 35 clutches from Eagle Summit, Alaska (Table 1; three years combined) were initiated prior to 1 June (the earliest estimated laying date was 28 May). Laying began in May during all three years, with mean initiation dates for each year (3 to 5 June) occurring earlier than the onset of laying for all but the three earliest clutches in the Wyoming sample. The earliest initiation date for 274 clutches in five years in Wyoming (both sites) was 4 June, including the exceptionally early year of 1987 (Hendricks 1993); the latest annual date for initiation of laying in the earliest clutch in the sample was 26 June in 1964 at Beartooth Pass. The proportions of clutches begun before and after 1 June differed significantly ($G = 46.4$, df = 1, $P < 0.001$) between the Alaska and Wyoming sites.

Annual mean clutch size across all latitudes was strongly negatively correlated with annual mean date of clutch initiation ($r = -0.950$, $n = 16$, $P < 0.001$; Fig. 1). In fact, 90% of the variation in annual mean clutch size was explained by mean day first eggs were laid at each site and year. The general relationship described by the regression equation was:

$$\text{clutch size} = 5.812 - 0.044(\text{laying date}). \quad (1)$$

The pattern was evident within a single site (Fig. 1: Wyoming data) as well as among sites. Laying date explained 83.8% of the variation in mean clutch size at the combined Wyoming sites ($r = -0.915$, $n = 8$, $P < 0.01$) and 89.8% of the variation at Beartooth Pass

alone ($r = -0.948$, $n = 5$, $P < 0.05$). The slopes of the Wyoming regression lines did not differ significantly ($F = 0.016$, df $= 1$ and 12, $P > 0.9$ and $F = 0.008$, df $= 1$ and 9, $P > 0.9$, respectively) from the slope for all other sites ($r = -0.979$, $n = 8$, $P < 0.01$). Thus, annual variation in the interaction between laying date and clutch size for individual populations appeared to be representative for all populations across the breeding range.

Discussion.—For American Pipits, laying date exerts a strong influence on annual clutch size. A common phenotypic pattern is expressed within populations (e.g. Beartooth Mountains, Wyoming) as well as among populations across the breeding range, and appears to be independent of latitude. Thus, equation 1 provides a robust model for predicting mean clutch size of any population of American Pipits. Three recognized subspecies (*A. r. rubescens* [Baffin Island]; *A. r. pacificus* [Alaska]; and *A. r. alticola* [California, Colorado, Wyoming]) were represented in the analyses. The uniformity of the relationship among populations of different subspecies also suggests that selection acts in a similar way on clutch-size traits throughout the breeding range of this species.

A surprising conclusion drawn from Figure 1 and the significant latitudinal increase in mean cumulative clutch size is that on average, pipits initiate nests earlier at higher latitudes than at lower latitudes. This pattern of egg laying is opposite to that for many other bird species in the Northern Hemisphere (e.g. Hussell 1972, Järvinen and Lindén 1980, Briskie 1995). The same "reverse" geographic pattern in mean clutch initiation date (i.e. earlier nesting in the north) has been observed in American Pipits in British Columbia (R. W. Campbell pers. comm.). Exceptions to this pattern occur, however (see Fig. 1). Mean laying date on Baffin Island in the Canadian High Arctic was 20 June in 1953, which was later than for Beartooth Pass in 1987 and 1988 ($\bar{x} = 11$ and 14 June, respectively). Weather during the early breeding season was harsh on Baffin Island in 1953 (Sutton and Parmelee 1954), whereas the Beartooth Mountains experienced mild winter and spring weather in 1987 and 1988 (Montana Annual Climatological Data, NOAA). Thus, extreme years could obscure patterns in clutch size unless data are pooled from more evenly distributed samples. In the case of the American Pipit, cumulative mean clutch sizes for California and Baffin Island (Verbeek and Hendricks 1994) probably do not represent the expected average clutch size for the respective latitudes largely because the majority of data for each locality was collected in "unusual" years.

The cues used by American Pipits to initiate nesting probably are different than for many temperate and equatorial species. Clutch initiation for bird species at mid-latitudes, where nest sites often are accessible year-round, has been correlated with in-

creasing insect abundance and phenology of leafing or "green-up" (Järvinen 1989a, Perrins 1991). In tundra habitats, green-up and increasing insect abundance are contingent upon the timing and rate of snowmelt (Billings and Mooney 1968, Maclean and Pitelka 1971, Norment 1992, Hendricks 1993). Thus, American Pipits need not anticipate when green-up will occur and insects will become abundant; each follows rapidly after the ground becomes free of snow, at which time potential nest sites become available (Verbeek 1970, Miller 1988, Hendricks pers. obs.). The inhibiting effect of snow cover on egg laying has been reported previously for other montane and tundra ground-nesting birds (e.g. Green et al. 1977, Morton 1978, Davies and Cooke 1983, Smith and Andersen 1985, Clarke and Johnson 1992, Norment 1992), including the most common arctic passerine, the Lapland Longspur (*Calcarius lapponicus*; Custer and Pitelka 1977, Fox et al. 1987).

Other factors could confound the pattern between laying date and clutch size described in this paper. First, clutch size can be positively correlated with female body size (e.g. Järvinen and Väisänen 1984), but the relationship is not universal (e.g. Gibbs 1988). Clutch size of American Pipits in Wyoming is positively correlated with female body mass at the time of incubation ($r = 0.413$, $n = 31$, $P < 0.03$; Hendricks unpubl. data). There is little evidence, however, for a trend in female body mass across the breeding range (Verbeek and Hendricks 1994); if anything, females appear to be slightly smaller at higher latitudes. Effects of female body size on clutch size are probably most evident within rather than between populations. Second, laying date could covary with elevation, with laying starting earlier in the north simply because sites are at low elevation. This argument could explain the typical pattern of larger clutches in cumulative samples from northern latitudes. However, it fails to account for variation in annual clutch size and laying date between sites at similar elevations (e.g. California vs. Colorado; Table 1, Fig. 1) or at single sites where elevation is constant (e.g. Beartooth Pass). Thus, it appears that elevation is neither a primary nor a confounding influence in the *annual* relationship between laying date and clutch size across the breeding range of this species. Third, differences in food (arthropod) abundance between mid- and high-latitude sites could affect clutch size directly. I am not aware of any studies contrasting arthropod biomass between arctic and alpine sites, although there is some evidence that differences among years in peak arthropod abundance do not always correspond to changes in mean clutch size (Hendricks 1993). The relationship between food abundance and clutch size across the range of this species needs further study.

American Pipits rarely initiate laying after mid-July, regardless of latitude (Hendricks 1993). None of the 376 clutches used in my analyses was begun after

17 July, and most (80.3%) were initiated prior to 1 July. Offspring produced from clutches laid in late July would not reach independence before September, by which time snowstorms are not uncommon. Furthermore, by mid-July males become reproductively refractory, with reduced testis size (Irving 1960, Verbeek 1970), and nutrients are diverted to feather growth with the onset of prebasic molt (Verbeek 1973). Therefore, the length of the breeding season is affected primarily by events in spring, and earlier snowmelt translates into a longer breeding season (although midsummer storms could terminate nesting prematurely in some years; Hendricks and Norment 1992). The timing of snowmelt relative to photoperiod could provide American Pipits with reliable environmental information that predicts the length of the upcoming breeding season, much as temperature does in northern Europe (Järvinen 1989b) for the Pied Flycatcher (*Ficedula hypoleuca*). Enlarged clutches in early years may be the result of better female condition (Martin 1987, Blem 1990) and selection favoring production of additional eggs due to increased probability of egg viability (Hendricks and Norment 1994), offspring survival, and recruitment (Rowe et al. 1994).

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Defining Cavity-associated Interactions Between Red-cockaded Woodpeckers and Other Cavity-dependent Species: Interspecific Competition or Cavity Kleptoparasitism?

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The endangered Red-cockaded Woodpecker (*Picoides borealis*) is unique in that it excavates cavities for roosting and nesting exclusively in living pines. Other cavity-dependent species, particularly Red-bellied Woodpeckers (*Melanerpes carolinus*) and flying squirrels (*Glaucomys volans*), commonly usurp these cavities (Ligon 1970, Jackson 1978, Neal et al. 1992, Loeb 1993, Kappes

and Harris 1995). Generally, these interactions are considered to be a form of interspecific competition (Ligon 1970, Jackson 1978, Carter et al. 1983, Harlow and Lennartz 1983, Rudolph et al. 1990, Loeb 1993, Kappes and Harris 1995, Winkler et al. 1995). I argue here that the term interspecific competition is inappropriate for describing heterospecific usurpation of roost or nest cavities because rather than being reciprocally negative (−,−), the interaction is negative for Red-cockaded

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