quickly disappeared. On several occasions they were seen catching small minnows (sp. ?), gleened from cracks in the ice, or from the ship's upwellings.

*Thick-billed Murre (*Uria lomvia*).*—Second most northern and abundant species noted. On 17 July, flocks (5–20 birds) circled the ship, but did not follow its wake. Although the flocks disappeared over thick pack ice, a few solitary individuals were noted en route to the Pole: on 19 July, one at 84°44′N, 33°59′E (P. Conway), and one at 85°30′N, 32°46′E. South from the Pole, one was noted at 87°22′N, 43°07′E on 22 July; one at 84°44′N, 33°59′E (P. Conway), and one at 85°30′N, 32°46′E on 23 July, two at 81°56′N, 32°46′E on 24 July. Small flocks were seen thereafter, notably near the Franz Josef islands. Thousands occupied precipitous cliffs at Calm Bay in the southwestern part of the Archipelago.

*Black Guillemot (*Cepphus grylle*).*—Uncommon, but the third most northern species recorded: on 24 July, over thick pack ice, one at 82°00′N, 38°47′E, one at 81°56′N, 39°49′E, one at 81°52′N, 40°01′E, and one at 80°55′N, 45°27′E. Numbers increased within Franz Josef Archipelago, especially near Cape Norway, Jackson Island.

*Ivory Gull (*Pagophila eburnea*).*—Observed only on two occasions over dense pack ice outside of the Franz Josef Archipelago where small numbers were noted. One was in the presence of a polar bear (*Thalarctos maritimus*) at 80°51′N, 40°40′E on 17 July. Most northern sighting (three birds) was at 80°55′N, 45°27′E on 24 July.

Three species of jaegers (*Stercorarius*) appeared to be fairly common over open waters of the Barents Sea (especially on 16 July at 72°54′N, 34°00′E, and on 28 July at 74°32′N, 37°24′E), but not over dense pack ice except within the Franz Josef Archipelago. Glaucous Gulls (*Larus hyperboreus*) were noted only within the Franz Joseph Archipelago, and Arctic Terns (*Sterna paradisaea*) only along the north coast of Norway.

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Hatchability of American Pipit eggs in the Beartooth Mountains, Wyoming.—Hatchability often is reported as the proportion of eggs laid that hatch. While this may be the demographic value of ultimate interest as an index of recruitment, such broad usage makes it difficult or impossible to identify more specific proximate factors affecting hatching and the extent that these may vary. Some studies note the paucity of data for comprehensive analyses of ecological and social factors influencing hatchability in wild birds (Rothstein 1973, Koenig 1982). Predation and abandonment frequently are major causes of egg loss prior to hatching, but egg infertility and embryo death may also contribute to hatching failure. These latter two conditions are of special interest because they (1) reduce potential individual reproductive success, (2) represent a substantial loss in reproductive investment by the female, and (3) can be expected to respond to selection. In theory, compensatory egg-laying could evolve in species with a high incidence of infertile eggs (Lundberg 1985), but this remains unsubstantiated and little explored. Because hatchability could be important in the evolution of reproductive traits, the topic deserves further study, especially for a wide variety of taxa and breeding environments.

Here, we examine hatchability of American Pipit (*Anthus rubescens*) eggs at high elevations. We define hatchability as the percentage of eggs present at hatching time that produce nestlings (see Koenig 1982). In particular, we describe annual and geographic variation in hatchability for a single population breeding over a 300 m elevation gradient. We also document the relation of hatchability to (1) median date of clutch initiation, (2) nest type, (3) egg size, and (4) clutch size. Finally, we compare our results with other species nesting in tundra environments and discuss common patterns.

Study sites and methods.—Data were collected during June–August of 1987–1989 at two sites in the Beartooth Mountains, Park County, Wyoming. One site was in alpine habitat with extensive tundra lying between the two summits of Beartooth Pass (Lat. 45°0'N, Long. 109°30'W, 3200 m elev). The second site was in subalpine meadows centered around Chain Lakes (2900 m elev), about 6.4 km SW of Beartooth Pass. Verbeek (1970) and Hendricks and Norment (1992) provide additional details of the respective sites.

Eggs broken during handling or found cracked (N = 6) are excluded from our samples. Analyses of clutch trends do not include clutches where one or more eggs disappeared prior to the date of hatching, nor are numbers of predated eggs included in egg samples and analyses, except for eggs known to have failed for other reasons prior to predation (e.g., nests found with older chicks and unhatched eggs, but predated before eggs were examined for infertility or embryo death). Hatching failure of examined eggs was attributed to infertility if there was no visible development of the blastodisc, or embryo death if a visible embryo was present. Our use of the term "addled" refers to both causes of hatching failure, and hatching failure as used in this paper refers to addled eggs only. We may have overestimated the proportion of addled eggs attributable to infertility by including eggs where decomposition of the yolk had begun, but eggs with decomposing yolks occurred in less than 5% of the total sample. If we found a nest containing chicks and no eggs, we assumed all eggs hatched, as pipits do not remove unhatched eggs from nests (pers. obs.), and loss of single eggs from nests was infrequent (Hendricks, unpub. data). A total of 692 American Pipit eggs from 135 clutches was used in our analysis.

Egg volumes (V) were calculated using Hoyt's (1979) equation: $V = 0.507LB^2$, where length (L) and breadth (B) were measured with a dial caliper to the nearest 0.1 mm. To maintain sample independence, all volumes in this paper are mean values for clutches, unless specified otherwise. In some cases volumes are based on a single egg per clutch. Preston (1968) showed that size measurements from a single egg per clutch tended to be representative of the entire set.

American Pipit nests were categorized as (1) rock nests: on the ground under overhanging rocks, or (2) sod nests: on the ground under overhanging vegetation or in erosion banks, hummocks, or pocket gopher burrows (see Verbeek 1970, 1981).

Statistical procedures throughout follow Sokal and Rohlf (1981), with variation given as the mean ± one standard deviation.

Results.—Forty-eight (35.6%) of 135 American Pipit clutches contained addled eggs. In the total sample of eggs (Table 1), 67 (9.7%) of 692 failed to hatch. Thus, hatchability for the Beartooth Mountains population was 90.3% during 1987–1989. Hatchability at Beartooth Pass during that period was 90.9% (380 of 418 eggs), which was greater than that for 1963–1964 (85.9%: 286 of 333 eggs; Verbeek 1970). Of the 67 addled eggs in 1987–1989, 40 (59.7%) were infertile, 18 (26.9%) contained dead embryos, and nine (13.4%) were of undetermined contents (Table 1). Twenty-eight (34.1%) of 82 pipit clutches at Beartooth Pass, and 20 (37.7%) of 53 at Chain Lakes, contained addled eggs ($G = 0.180$, df = 1, $P > 0.5$); Verbeek's (1970) data could not be used in this analysis. Proportions varied between

TABLE 1

CAUSES OF HATCHING FAILURE AND HATCHABILITY IN AMERICAN PIPIT EGGS

	Total eggs[a]	Infertile	Embryo death	Unknown	Hatchability (%)
Beartooth Pass (3200 m)					
1987	127	7	4	0	91.3
1988	145	7	0	6	91.0
1989	146	10	4	0	90.4
Chain Lakes (2900 m)					
1987	108	7	3	0	90.7
1988	85	7	3	3	84.7
1989	81	2	4	0	92.6
Sites combined					
1987–1989	692	40	18	9	90.3

[a] Not including six eggs cracked during handling, by adults, or nests predated during incubation.

years by as much as 14.1% at Beartooth Pass ($G = 1.162$, df = 2, $P > 0.5$) and 27.9% at Chain Lakes ($G = 2.850$, df = 2, $P > 0.1$). Although these results do not show statistically significant variation, small sample size may have led to the inflated P value for Chain Lakes. The difference between sites was greatest in 1988 ($G = 2.934$, df = 1, $P < 0.1$), when 27.6% of Pass clutches and 52.9% of Chain Lakes clutches contained addled eggs. Hatchability of pipit eggs (Table 1) was virtually the same (90.2–92.6%) in all three years at both sites, except at Chain Lakes during the hot and dry summer of 1988, when hatchability was 7.2% less than the 1989 maximum.

Hatchability at Beartooth Pass was negatively correlated with the median date of egg-laying for the population (Fig. 1). In 1963 and 1964, when egg-laying was 10–18 d later (medians = 28–29 June) than 1987–1989 (medians = 10–18 June), hatchability (data extracted from Fig. 2 and Table 7 in Verbeek 1970) was 3.9–4.9% less than the minimum during 1987–1989. Comparable data were not available for Chain Lakes.

Twelve (34.3%) of 35 rock nests and 30 (37.5%) of 80 sod nests contained addled eggs ($G = 0.108$, df = 1, $P > 0.5$). For a smaller sample of nests with addled eggs of identified contents, ten rock nests (76.9%) contained infertile eggs, and three (23.1%) contained dead embryos, whereas 14 sod nests (58.3%) contained infertile eggs and ten (41.7%) had dead embryos ($G = 1.326$, df = 1, $P > 0.1$). Nest type did not influence hatchability, but dead embryos appeared in rock nests less frequently when addled eggs were present. Again, small sample size probably inflated the P value.

The difference between mean volumes of clutches with some (2177 ± 185 mm^3, N = 40) and no hatching failure (2195 ± 153 mm^3, N = 38) was slight ($t = 0.469$, df = 76, $P > 0.5$). The smallest egg was addled in ten (41.7%), and the largest egg in eight (33.3%), of 24 clutches where hatching failure occurred and all egg volumes were known. If hatching failure was a random occurrence within a clutch, then the expected number of smallest or largest eggs to fail (E_s) would be the product of the average probability of the smallest (largest) egg failing (P_s) and the total number of clutches in the sample (N), or $E_s = (P_s)(N)$. In this case, mean clutch size was 5.1 for the sample, so $P_s = 1/5.1 = 0.196$, and $E_s = 0.196 \times 24 = 4.7$. This value assumes only one egg failing per clutch. However, 1.6 eggs failed per clutch in the above sample, so the value calculated should be multiplied by 1.6,

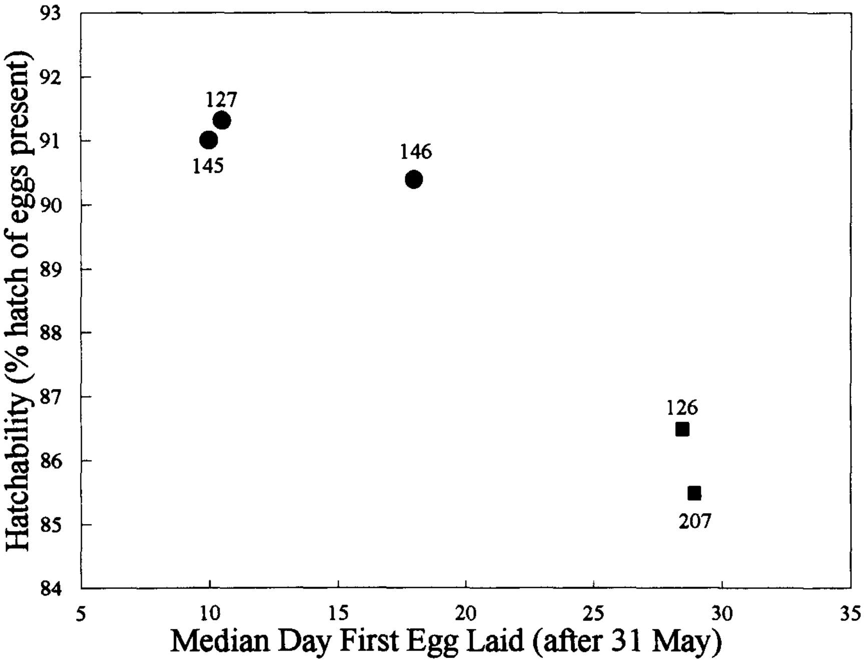

FIG. 1. Median day of clutch initiation (after 31 May) and hatchability for American Pipits nesting at Beartooth Pass (3200 m), Park County, Wyoming. Points represent single breeding seasons (squares for 1963–1964, circles for 1987–1989), and corresponding numbers are total eggs in each sample; data for 1963–1964 are extracted from Verbeek (1970).

and E_s becomes 7.5. This is only slightly different than the number of smallest ($G = 1.154$, df = 1, $P > 0.2$) or largest ($G = 0.053$, df = 1, $P > 0.5$) addled eggs. The proportion of smallest and largest addled eggs in this sample was similar ($G = 0.360$, df = 1, $P > 0.5$), further indicating that hatchability was independent of egg size.

However, egg volume was important in determining the type of hatching failure. Mean volume of infertile eggs (2128 ± 203 mm^3, N = 24 clutches) was 6.3% less than eggs with dead embryos (2270 ± 167 mm^3, N = 12 clutches; $t = 2.091$, df = 34, $P < 0.05$). Infertile eggs ranged from 1809–2488 mm^3 (N = 14) at Chain Lakes and 1635–2636 mm^3 (N = 24) at Beartooth Pass. Respective ranges for eggs with dead embryos were 1822–2601 mm^3 (N = 10) and 2136–2555 mm^3 (N = 8).

Clutches containing addled eggs were not appreciably larger (5.2 ± 0.7, N = 47) than those with none (5.0 ± 0.9, N = 87; $t = 1.042$, df = 133, $P > 0.2$). In nests with addled eggs, clutch size did not differ between those containing infertile eggs (5.3 ± 0.6, N = 24) and dead embryos (5.3 ± 0.5, N = 13; $t = 0.101$, df = 35, $P > 0.9$). The proportion of clutches experiencing some hatching failure increased slightly with clutch size (by 9.5%) for four- to six-egg clutches (Table 2), but the differences were not significant ($G = 0.528$, df = 2, $P > 0.5$). Hatchability remained constant over that same range of clutch sizes.

Of 48 clutches with some hatching failure, 14 (29.2%) involved more than one egg, but the occurrence of multiple addled eggs varied little from four-egg (33.3%) to six-egg

TABLE 2

CLUTCH SIZE OF AMERICAN PIPITS AND THE NUMBER OF CLUTCHES WITH UNHATCHED EGGS

	Number of unhatched eggs/clutch[a]					Proportion hatch failure	
	0	1	2	3	4	Clutches[b]	Eggs
Clutch size							
3	5[c]	1	—	—	—	0.167	0.056
4	14	4	2	—	—	0.300	0.100
5	44	18	7	1	—	0.371	0.100
6	23	11	1	2	1	0.395	0.101
7	1	—	—	—	—	0.000	0.000

[a] Not including nests with cracked eggs.
[b] With one or more unhatched eggs.
[c] Number of clutches.

(26.7%) clutches ($G = 0.120$, df = 2, $P > 0.5$). Also, the observed distributions of addled eggs within four- to six-egg clutches differed little from expected (binomial tests; $P > 0.2$). In only one of nine clutches containing multiple addled eggs of known contents was hatching failure due to both infertility and embryo death ($G_{\text{adj.}} = 5.869$, df = 1, $P < 0.05$). There were no known cases where entire unabandoned clutches failed as a result of infertility or embryo death or both (Table 2).

Discussion.—Several ecological and social patterns in hatchability have been identified for natural populations. Koenig (1982) found hatchability to be a function of nest type (open or cavity), diet, latitude, and the degree of sociality in an analysis of 155 studies representing 113 species.

Overall hatchability (Table 1; 90.3%) of American Pipit eggs at our two sites fell within the range of 80.4–94.0% for other passerines (Ricklefs 1969, Dixon 1978, Morin 1992), and was almost Koenig's (1982) predicted percentage for the latitude of our study sites. Hatchability was much lower (84.7%) below treeline at Chain Lakes in 1988 than for other years at either site during our three-year study, and was the only sample for which hatchability was <90.0%. Increased incidence of addled eggs at Chain Lakes in 1988, the summer of extensive wildfires in Yellowstone National Park about 35 km away, may have been the result of hot and exceptionally dry conditions for the region (Singer et al. 1989). Chain Lakes, 300 m lower than Beartooth Pass, normally experiences daily maximum temperatures 2–4°C higher (Hendricks and Norment 1992). High temperatures are injurious to developing embryos, and exposure of eggs to direct sunlight (when females are off of the nest) can kill embryos even though air temperatures may be relatively cool (Zerba and Morton 1983, Morton and Pereyra 1985, Webb 1987); ground-level temperatures at high elevations can exceed air temperatures by >20°C (Swan 1952, Hadley 1969) and may add thermal stress to incubating females of ground-nesting species, such as the American Pipit. It is possible that several eggs considered infertile in 1988 actually contained embryos that died in the first day or two of development and were misclassified. Regardless of this possibility, there was an association between a greater incidence of addled eggs and unusually warm weather at the subalpine site.

In contrast with Rothstein (1973), at Beartooth Pass we found a higher incidence of addled eggs produced by American Pipits during years with delayed egg-laying and lingering snowpack (Fig. 1). This pattern might be related to differences in food availability or quality, or the maintenance energy and protein demands on females during and after egg-laying (see Martin 1987). Unfortunately, direct measures of food abundance at Beartooth Pass during the breeding season are not available for 1963–1964; maximum arthropod abundances did not differ greatly during 1987–1989 (Hendricks, unpub. data). During the initial week of laying in 1987–1989, mean clutch size was identical (5.5; Hendricks, unpub. data) and hatchability ranged from 90.4–91.3%. In 1963–1964, when hatchability was <87%, clutch size during the first nine-day laying period was 4.7 (Verbeek 1970). Females waiting to lay for extended periods (as in 1963–1964) may lose important energy and protein reserves, resulting in the production of a greater proportion of lower quality or infertile eggs (see Blem 1990). Also, females may have to spend more time foraging away from nests to satisfy maintenance energy demands because of cooler initial and average conditions during late years. This could result in eggs cooling to lethal temperatures from inefficient incubation (Pinowski 1968). Hatchability of Harris' Sparrow (*Zonotrichia querula*) eggs in the Northwest Territories of Canada was lowest (78.9%) during a year when conditions during laying were cooler and wetter than in other years (Norment 1992).

Similar to other studies (Koenig 1982, Bancroft 1984, Briskie and Sealy 1990), we found that hatchability and size of American Pippit eggs were not correlated. Volume varied significantly between sites in 1989 (Hendricks 1991) but did not correspond to a large difference (2.2%) in the occurrence of addled eggs. Conversely, the difference in hatchability between sites increased to 6.3% in 1988, but the difference in mean egg volume was not significant (t = 0.040, df = 45, $P > 0.9$; Hendricks, unpub. data). This is consistent with the hypothesis that temperature, rather than egg size, had a deleterious effect on hatchability of pipit eggs at Chain Lakes in 1988.

Unlike hatchability, the contents of addled eggs were related to egg size; infertile eggs were smaller than eggs containing dead embryos. Perhaps smaller eggs were more likely to lack membranes or the proper ratio of albumen to yolk needed for fertilization and development, as is the case with runt eggs (e.g., Koenig 1980a, b), but infertility was probably a function of several factors. Absolute size (volume) was not the sole determinant of infertility, as the size range of infertile pipit eggs (1635–2636 mm^3) was large and overlapped the range of fertile eggs (see Hendricks 1991). Our results were unaffected by runt eggs; volume of the smallest egg in our sample (1635 mm^3; infertile with a yolk) was 85.9% of the clutch mean for the other five eggs, all of which hatched. No egg fell under Koenig's (1980a) 75% relative size criterion for runts.

Infertile eggs comprised a greater proportion (5.8%) of our three-year American Pipit sample from high-elevation tundra than the 1.2–2.6% for several passerine species nesting in high-latitude tundra at Churchill, Manitoba during a four-year study (Jehl 1971). Hatchability for Lapland Longspurs (*Calcarius lapponicus*) at Barrow, Alaska, also a high-latitude tundra site, was 93.0% (88.8–98.5%) during a seven-year study (Custer and Pitelka 1977), a slightly better performance than for Beartooth pipits (90.3%) and greater than the range of values at Beartooth Pass (Fig. 1). However, longspur hatchability during two years of very different weather in West Greenland was 85.4–86.6% (Fox et al. 1987). Hatchability of Harris' Sparrows in the Northwest Territories of Canada averaged 87.6% (78.9–93.4%) during three years (Norment 1992). These data show that hatchability can be heterogeneous among years at one locality, and that conclusions on species-specific hatchability based on small samples of eggs or breeding seasons could be misleading. Nevertheless, overall hatchability appears to be similar for passerines breeding in mid-latitude and high-latitude alpine and Arctic tundra.

Hatchability tends not to be a function of elevation (Carey et al. 1982, Koenig 1982), although the number of studies on single species is small. Our data for American Pipits over a 300 m elevation gradient showed that hatchability was relatively uniform during breeding seasons of cool weather. However, hatchability below treeline during hot years may be lower than in the alpine, as was the case in the Beartooth Mountains in 1988, because temperature maxima are more extreme in high-elevation subalpine meadows. It would be interesting to see if hatchability is increased for American Pipits nesting at low-elevation high-latitude sites.

Orientation of Beartooth pipit nests protects eggs from exposure to direct sunlight and its detrimental effects on embryo development (Verbeek 1981, Zerba and Morton 1983, Morton and Pereyra 1985), and hatchability was unrelated to nest type. However, in spite of small samples, eggs in sod nests appeared more susceptible to embryo death. If this is really the case, overcooling during periods of foul weather could contribute to this pattern (see Hendricks and Norment 1992); lowest hatchability (78.9%) of Harris' Sparrows, which build cup nests on the ground under overhanging vegetation, occurred when weather during laying was cooler and wetter than in other years (Norment 1992). Overhanging grasses and turf provide less overhead protection from precipitation to nests than does rock, even though grass is a better insulator (Collias and Collias 1984).

Koenig's (1982) broad analysis showed that species building ground and open-cupped nests had greater hatchabilities than shrub, tree, and closed (cavity) nesters. Koenig (1982) suggested that a greater proportion of inexperienced females, with reduced hatchabilities during first breeding attempts, might be included in samples for species relatively protected from predators, such as cavity-nesting woodpeckers; experienced, older females are less likely to be predated in species normally experiencing high rates of predation, such as ground nesters. This tells us little about single species, however, and emphasizes the need for further studies on the influence of nest placement on intraspecific geographic patterns of hatchability.

Hatchability was unrelated to clutch size in our study of American Pipits (Table 2), a result also observed for other species (Rothstein 1973, Koenig 1982, Lundberg 1985, but see Briskie and Sealy 1990). Also, the proportion of clutches containing addled eggs increased only slightly with clutch size, and multiple addled eggs appeared in nearly equal frequencies among four- to six-egg clutches. If clutch size has any influence on hatching success of pipit eggs, the effect is apparently minor.

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