FACTORS INFLUENCING AGE-RELATED REPRODUCTIVE SUCCESS IN THE WILLOW PTARMIGAN

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ABSTRACT.—In many species, adult birds lay earlier and have higher reproductive success than do yearlings. We found no difference, however, between adult and yearling female Willow Ptarmigan (*Lagopus lagopus alexandrae*) in date of clutch initiation, clutch size, hatching success, number of fledged young, or territory size. Adult females defended their broods more vigorously, and more were observed with broods, a situation suggesting that more yearlings lost their eggs or young and did not renest. Pairs composed of two adults produced more fledged young than did pairs composed of two yearlings, but clutch size and date of clutch initiation were similar in the two groups. We suggest that the following factors may allow yearlings to reproduce almost as successfully as adults: (1) a reduction in competition with adults for territories because of high population turnover, (2) the presence of extensive male parental care and precocial young, and (3) a dependence on a food source that is readily available and can be obtained without specialized foraging skills. *Received 8 August 1983, accepted 28 March 1984.*

HYPOTHESES concerned with the factors that influence the onset of breeding in birds focus at three different levels: (1) on general environmental cues, such as changes in photoperiod or rainfall, that explain differences in timing among species or among geographical areas (reviewed by Wingfield 1983); (2) on specific extrinsic factors, such as weather or the availability and quality of food, that explain differences in timing among populations or among years (e.g. Perrins 1970, Zwickel 1975, Greenlaw 1978); and (3) on intrinsic factors, such as age and experience of the female or the male, or on genetic factors that explain differences in timing among individuals within populations (e.g. Perrins and Moss 1974, Finney and Cooke 1978, Harvey et al. 1979, van Noordwijk et al. 1980). In this paper we concentrate on intrinsic factors, specifically the influence of age on reproductive performance.

Age and experience have long been considered to be important variables in explaining not only the timing of breeding but the reproductive output as well. In many species, older birds lay earlier and have higher reproductive success than first-time breeders (e.g. Nelson 1966, Crawford 1977, Blus and Keahey 1978, Middleton 1979). This has been attributed to the inexperience of young birds in locating food required for egg formation (Lack 1968) and to social inhibition of young birds when they compete with adults for breeding sites (Wynne-Edwards 1962). In some species, however, first-time breeders do just as well as older birds (e.g. Leinonen 1973, Myrberget 1967).

In this paper, we compare timing of breeding, reproductive output, and territory size of adult and yearling Willow Ptarmigan (*Lagopus lagopus alexandrae*) of both sexes. We then compare Willow Ptarmigan with other species of grouse and discuss the effects of mating-system type, population demography, and other factors on the timing of breeding and reproductive output of young birds.

STUDY AREA

This study was conducted in an area of subalpine tundra on the flats of the Chilkat Pass, northwestern British Columbia, Canada (59°50'N, 136°30'W). Three plots, each 1 km apart and totalling an area of 320 ha, were worked intensively (Hannon 1983), and areas between plots were worked less intensively. Vegetation consisted of an overstory of scrub willow (*Salix* spp.), birch (*Betula glandulosa*) and shrubby cinquefoil (*Potentilla fruticosa*) and an understory of bryoids, graminoids, and perennial forbs. The climate is characterized by heavy snowfall in winter, frequent light to moderate rain the rest of the year, and moderate to high winds year round. Snow up to 1.5 m deep covered the area when fieldwork began in April and usually melted by the end of May.

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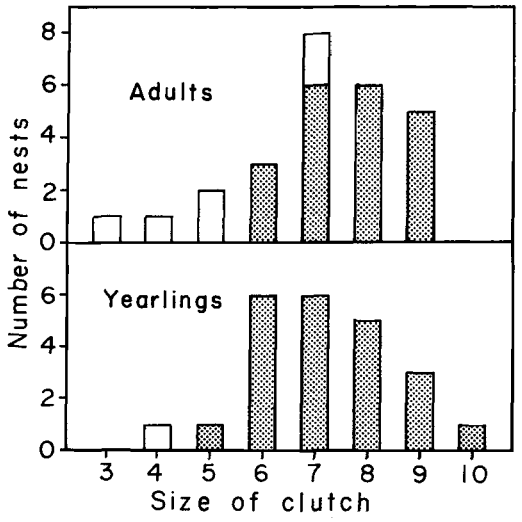

Fig. 1. Frequency distributions of clutch sizes of adult and yearling female Willow Ptarmigan (unshaded areas indicate probable renests).

Methods

The study period extended from April to August each year from 1979 through 1981. Ptarmigan were captured in nets or noosed and were individually color-banded. Birds were classed as either adult (22 months or older) or yearling (up to 13 months old) on the basis of pigmentation of the eighth and ninth primaries (Bergerud et al. 1963). We censused birds on the plots about twice each week and plotted their territories by noting locations of boundary disputes, territorial calling, and positions where birds turned back when pursued by an observer. The annual mortality rate was estimated by calculating return rates the next spring of color-marked birds on the intensively worked plots only.

Nests were located by searching around the roosts of males (males sit close to the nests and act as sentinels) or were found by a pointing dog during routine census. Nests were checked and eggs counted every 2 or 3 days until eggs hatched. Hatching success refers to the percentage of all eggs that hatched.

Broods were located by a trained pointing dog. The ages of juveniles were estimated by the method of Bergerud et al. (1963), and dates of hatch were estimated by backdating. Young were marked with metal patagial tags and weighed to the nearest gram. Chicks with an egg tooth were considered to be less than a day old. The date of clutch initiation was calculated by subtracting from the date of hatch the length of time needed to lay (7 days) and incubate (21 days) a clutch of mean size (Myrberget 1967). Hatch dates from different years and plots were combined by adjusting them to the same modal date of hatch. Nests that hatched late in the season and formed a second peak in the hatch-date distribution were considered to be renests (Zwickel 1977). The number of fledged chicks per brood (brood size) was counted by searching with a trained pointing dog and counting the number of juveniles that flushed. Chicks usually began to fly at 11 or 12 days of age, and those used in the analysis varied from 11 to 33 days of age.

Males and females accompanying broods were each assigned a brood-defense score from 0 to 5 based on the intensity of their distraction display and the closeness of their approach to the observer and dog. A score of 0 indicated no defense, a score of 5 a physical attack. We used only scores from the first encounter with each brood and included only cases in which juveniles had not yet begun to fly.

Statistical comparisons of the breeding success of adults and yearlings were based on the null hypothesis that adults would be more successful than yearlings. Tests were one-tailed, and we considered probabilities less than 0.05 to be significant. Sample sizes for each parameter measured were not equal, because all birds were not located during each stage of the breeding cycle.

Results

Age of the female and reproductive success.—The increased age and experience of adult hens did not improve their reproductive output over that of yearlings. Clutch sizes, hatching success, and the percentage of nests found that had some or all eggs missing (presumably due to predation) were similar for both age classes of hens (Fig. 1, Table 1). Dates of clutch initiation were sim-

Table 1. Comparison of nesting parameters for adult and yearling female Willow Ptarmigan at Chilkat Pass, 1979–1981 (*n*).

Parameters	Adults	Yearlings	Test[a]	*P*
Mean clutch size ± SE	7.1 ± 0.31 (26)	7.1 ± 0.29 (23)	$t = 0.12$	< 0.5
Percentage of eggs hatched	80.4% (184)	76.2% (164)	$G = 0.91$	< 0.3
Percentage of nests depredated	15.4% (26)	26.1% (23)	$G = 0.86$	< 0.5

[a] t = unpaired t-test; G = G-test for independence with Williams' correction.

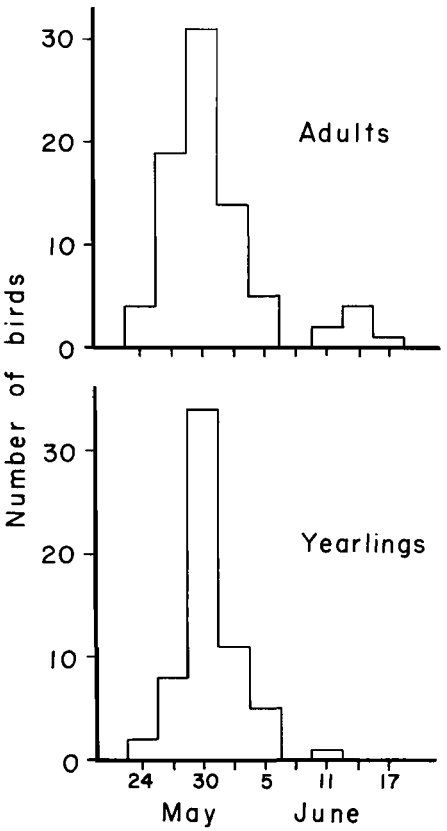

Fig. 2. Frequency distributions of dates of clutch initiation by adult and yearling female Willow Ptarmigan.

ilar for adults and yearlings (Fig. 2, $U = 2{,}305$, $P = 0.3$), although more adults than yearlings began to lay after 8 June (9% and 2%, respectively, $G = 3.54$, $P < 0.05$). Late nests were probably the result of renesting and often had fewer eggs than earlier nests (Fig. 1). Thus, adults may have renested more frequently than yearlings.

Chicks produced by adult hens weighed more at hatch than those produced by yearlings; the difference was so slight, however, that it was probably not biologically significant. Adults were slightly, but significantly, more aggressive in defense of their young (Table 2). Of hens censused in spring, a higher percentage of adults were later located with broods than were yearlings (Table 2). Of yearlings not resighted with a brood, 29% were located alone during the brood season, and, of the remainder, 29% were resighted the next spring. These yearlings probably lost all of their eggs or young to predators or other mortality factors and did not renest. Presumably, the yearlings not accounted for either died or emigrated from the study area. Both age classes of hens produced similar numbers of fledged chicks when only hens located with broods were considered (Table 2).

Adult and yearling hens also defended territories (Hannon 1983) of similar size (Table 2). There was no correlation between the territory sizes of females and the number of young fledged per territory ($r = 0.04$, $n = 17$).

Age of the male and reproductive success.—Adult and yearling males defended territories of similar size and were equally aggressive in the defense of young, but adults produced more fledged young than did yearlings (Table 3). All males that were identified as territorial but unmated were yearlings ($n = 15$). [Large numbers of nonterritorial birds of both sexes were also present, mainly yearlings (Hannon 1983).]

Age of the pair and reproductive success.—Of 182 pairs in which both birds were marked, 42% were both adults, 25% were both yearlings, 16% were composed of an adult female and yearling male, and 17% of a yearling female and adult male. The effect of male and female age on reproductive success was determined with a one-way analysis of variance (Table 4). Neither

TABLE 2. Comparisons of mean weights of chicks at hatch, brood-defense scores, numbers of chicks fledged, percentage observed with brood, and mean territory size of adult and yearling females [mean ± SE (n)].

Parameters	Adults	Yearlings	Test	P
Weight of chicks (g)	14.6 ± 0.11 (116)	14.3 ± 0.13 (69)	$t = 2.0$	<0.03
Brood defense score	3.2 ± 0.12 (78)	2.9 ± 0.11 (57)	$t = 2.0$	<0.03
Number of chicks fledged	5.2 ± 0.27 (54)	4.6 ± 0.30 (41)	$t = 1.4$	<0.1
Percentage observed with brood	79.1% (91)	66.2% (65)	$G = 3.2$	<0.05
Territory size (ha)	2.9 ± 0.17 (28)	2.7 ± 0.14 (30)	$G = 0.9$	<0.2

TABLE 3. Comparison of number of chicks fledged, brood-defense scores, and territory sizes of adult and yearling male Willow Ptarmigan [mean ± SE (*n*)].

Parameters	Adults	Yearlings	*t*	*P*
Number of chicks fledged	5.3 ± 0.30 (44)	4.4 ± 0.35 (27)	1.76	<0.05
Brood-defense score	2.6 ± 0.17 (59)	2.6 ± 0.16 (51)	0.33	<0.5
Territory size (ha)	2.8 ± 0.18 (57)	2.4 ± 0.14 (63)	1.42	<0.1

clutch size nor date of clutch initiation varied significantly among the four groups. Numbers of young fledged (brood size) did vary significantly with the age of the pair, however. Old pairs were more successful than yearling pairs (Duncan's multiple range test). Pairs of mixed age were intermediate and not significantly different from either adult or yearling pairs.

DISCUSSION

Willow Ptarmigan differ from most other species studied in that females breeding for the first time are similar to adults in terms of territory size, date of clutch initiation, clutch size, hatching success, and brood size. A higher percentage of adults was observed with broods, but whether this was due to differential predation on the nests or young of yearlings or to adults renesting more often is not known. Pairs comprised of two adults produced larger boods than did yearling pairs. The combined experience of adult pairs may have helped to reduce loss of young but did not influence clutch size or date of clutch initiation. Adult hens were also more aggressive in the defense of the brood. Myrberget (1967) found that adult Willow Ptarmigan (*L. l. lagopus*) in Norway had a tendency to conceal their nests better and were more aggressive in the defense of their young than were yearlings; none of these behavioral differences, however, resulted in higher nesting success or larger brood sizes for adults.

Yearling males defended territories of the same size as those of adults and were equally aggressive in the defense of young, but they produced fewer fledged young. All territorial adults obtained mates, but some territorial yearlings did not. These unmated yearling males had shorter wings, weighed less, and held smaller territories than did mated yearlings, and they may have been subordinate birds (Hannon 1983).

Among grouse species in general, there is a tendency for yearling hens to lay smaller clutches later than do adults but to have similar nesting success (Table 5). Within the species that form pair bonds, White-tailed Ptarmigan (*Lagopus leucurus*) resemble promiscuous species more than they do other monogamous grouse in that adults do better than yearlings. Rock Ptarmigan (*Lagopus mutus*) appear to be intermediate: clutch size is the same for adults and yearlings, but adults lay earlier (Table 5). Willow Ptarmigan are thus unusual among grouse, in that reproductive parameters of adult and yearling females are quite similar, and this is true for three different populations and subspecies (Table 5).

What could explain the age-related differ-

TABLE 4. Effect of age of hen and cock on clutch size, date of first egg, and number of chicks fledged [mean ± SE (*n*)].

Age of hen	Age of cock	Clutch size	Date of first egg[a]	Chicks fledged
Adult	Adult	7.2 ± 0.34 (19)	8.3 ± 0.43 (43)	5.5 ± 0.36 (33)
Adult	Yearling	6.4 ± 0.99 (5)	9.6 ± 0.57 (20)	5.2 ± 0.59 (10)
Yearling	Adult	6.4 ± 0.51 (5)	9.5 ± 0.68 (17)	4.6 ± 0.47 (11)
Yearling	Yearling	6.9 ± 0.39 (12)	9.0 ± 0.48 (30)	4.0 ± 0.40 (17)
F ratio		0.63	1.41	2.65
P =		0.60	0.24	0.05

[a] Data exclude possible renests; Day 8 = 31 May.

TABLE 5. Comparison of reproductive parameters and annual adult mortality rates among age classes for seven species of grouse.[a]

Mating system	Date first egg	Clutch size	Nesting success	Brood size	Mortality	Reference
Species with pair bonds						
Willow Ptarmigan						
Lagopus lagopus lagopus	A = Y	A = Y	A = Y	A = Y	66%	Myrberget 1967, 1972
L. l. alleni	A = Y	A = Y	—	—	72%	Bergerud 1970
L. l. alexandrae	A = Y	A = Y	A = Y	A = Y	60%	This study
Rock Ptarmigan						
L. mutus	A < Y	A = Y	—	—	40–74%	Weeden 1965; Modafferi 1975
White-tailed Ptarmigan						
L. leucurus	—	A > Y	A > Y	—	36–45%	Choate 1963; Braun & Rogers 1971; Giesen et al. 1980
Promiscuous species						
Sage Grouse						
Centrocercus urophasianus	A < Y	A > Y	A > Y	—	42–65%	Dalke et al. 1963; Wallestad & Pyrah 1974; Wallestad 1975; Braun (unpubl. data)
Blue Grouse						
Dendragapus obscurus	A < Y	A > Y	A = Y	—	30%	Zwickel 1975, 1977, 1980
Spruce Grouse						
D. canadensis franklinii	—	A > Y	A = Y	A = Y	30%	Keppie 1975
D. c. canace	—	A > Y	A = Y	A = Y	—	Keppie 1982
Ruffed Grouse						
Bonasa umbellus	—	A > Y	—	—	54%	Bump et al. 1947

[a] A = Y: no difference between age classes; A > Y: adults do better than yearlings; A < Y: adults before yearlings; —: data not available.

ences in reproductive parameters between Willow Ptarmigan and other grouse? We will first consider explanations for females and then for males. Willow Ptarmigan usually pair monogamously, and males contribute more parental investment than do males of any other grouse species (Wittenberger 1978). For example, in Rock and White-tailed ptarmigan, females forage on the territories of males before laying, and males act as sentinels at the nest but do not contribute to care of the young. In promiscuous species, females and males associate briefly for copulation, but males do not contribute any form of parental care. Male Willow Ptarmigan provide vigilance for hens as they forage on territories, act as sentinels at the nest, and accompany the brood and defend the young. Perhaps this extensive male assistance compensates for physiological and behavioral differences that could exist between adult and yearling hens. Older males improved the reproductive success of hens in this study.

A second factor that distinguishes Willow Ptarmigan from most other grouse species is the high turnover rate of the population. Annual adult mortality ranges from 60 to 72%, comparable only to Rock Ptarmigan and Sage Grouse (*Centrocercus urophasianus*) and much higher than most other species (Table 5). This high adult mortality opens up large amounts of available area for territories for yearlings and reduces competition with adults for breeding space. Thus, the inhibition or delay of breeding through social interactions with adults, a phenomenon suggested to exist in species with lower adult mortality (Hannon et al. 1982),

would be alleviated. Social factors have been implicated in delayed breeding in other species (Carrick 1963, Robel and Ballard 1974, Crawford 1977).

Male Willow Ptarmigan also differ from males of other species of grouse in that yearlings are similar to adults in most aspects. Yearling male White-tailed Ptarmigan rarely establish territories, and, if they do, their territories are smaller than those of adults, and the yearlings usually remain unmated (Choate 1963). Yearling males of promiscuous species are usually not territorial, and most do not breed (Wiley 1974). Lewis and Zwickel (1980) reported that yearling male Blue Grouse did not take territories even though space was available and they were physiologically able to breed. However, the available habitat was of poorer quality and the chance of attracting a hen lower (Lewis and Zwickel 1980, 1981). Delayed breeding by male Blue Grouse (*Dendragapus obscurus*) may have evolved because nonterritorial males have low mortality rates (20%) and, thus, may gain more by waiting for high-quality sites than by settling earlier on low-quality sites (Lewis and Zwickel 1982). In *Lagopus lagopus* in Scotland, nonterritorial birds suffer high mortality (Jenkins et al. 1963), and, because of the high turnover rate of the population, many territories are available each spring. Delayed breeding in males would not be expected to occur in populations with these characteristics.

The extent of parental investment provided by males and the degree of competition for breeding space may explain age-related differences in breeding among grouse as outlined above. Many passerine species, however, have a high population turnover, are monogamous, and have extensive male parental care, yet yearling females of these species are still delayed in breeding. Additions of food can advance the first egg date for yearlings more than for adults in some of these species (reviewed by Ewald and Rowher 1982). Inexperience may have more of an effect in species that depend on food sources that are difficult to locate, capture, or handle or are limited in time and space. Young birds may be less successful at foraging than older birds (Orians 1969, Recher and Recher 1969). Grouse, however, are herbivorous and feed mainly on leaves, buds, or twigs that appear to be readily available. Thus, the effects of inexperience on the procurement of food could be reduced. In addition, grouse have precocial young, and the loss of young through adults' inexperience in finding food would also be reduced, when compared with species with altricial young. Prior experience may also be important in species that build complicated nests or those that experience high levels of nest predation and rely on nest concealment or complicated distraction displays. Thus, there are a number of factors that could affect the importance of previous experience in improving breeding success. Further work on the determinants of age-related differences in breeding success is needed to ascertain the relative importance of these factors.

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