

SIMULTANEOUS MULTIPLE CLUTCHES AND FEMALE BREEDING SUCCESS IN MOUNTAIN QUAIL

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Abstract. To evaluate the contribution of simultaneous clutches to breeding success in female Mountain Quail (*Oreortyx pictus*), we located nests of radio-marked male and female Mountain Quail in west-central Idaho from 1992 to 1995 and estimated rates and parameters of nesting success. In our sample, 29 females, 19 males, and 4 quail of unknown sex, including 12 apparently monogamous pairs, incubated nests. Using logistic regression, we found that constant survival and sex were the best-supported models to explain nest success for 45 nests of known age. Odds of success for male-incubated nests were 1.7-times (95% CI: 0.4–7.9) greater than for female-incubated nests. Mean clutch size for first nests was 11.8 (range: 6–16) and clutches incubated by males (12.6 ± 0.3 eggs) were significantly larger than female-incubated clutches (11.4 ± 0.4 eggs). Mean hatching date for all nests was 2 July (range: 10 June–23 July). Two of six females whose nests were depredated re-nested. Paired females produced an average of 24 eggs (range: 20–28). Mean hatching date for nine paired males was 30 June \pm 3 days and 3 July \pm 3 days for females. The estimated average number of days spent on nesting activities for nine successfully hatched pairs was 59 (range: 54–64). All 12 paired females hatched at least eight chicks from both clutches. Our findings indicate that simultaneous clutches in Mountain Quail ensures breeding success in females under conditions that may not be amenable to other forms of multiple brooding.

Key words: biparental care, female breeding success, Idaho, Mountain Quail, *Oreortyx pictus*, re-nesting, simultaneous multiple clutches.

Nidadas Múltiples Simultáneas y Éxito Reproductivo de las Hembras en *Oreortyx pictus*

Resumen. Para evaluar la contribución de las nidadas simultáneas al éxito reproductivo de las hembras de la especie *Oreortyx pictus*, localizamos los nidos de machos y hembras marcados con radio transmisores en el oeste-centro de Idaho entre 1992 y 1995, y estimamos tasas y parámetros relacionados con el éxito reproductivo. Nuestra muestra de aves que se encontraban incubando estuvo compuesta por 29 hembras, 19 machos y cuatro individuos de sexo desconocido, incluyendo 12 parejas aparentemente monógamas. Mediante una regresión logística determinamos que los modelos de supervivencia constante y sexo fueron los que mejor explicaron el éxito de 45 nidos de edad conocida. Las probabilidades de éxito para los nidos incubados por machos fueron 1.7 veces mayores (IC 95%: 0.4–7.9) que las de los nidos incubados por hembras. El tamaño promedio de la nidada para los primeros nidos fue 11.8 huevos (rango: 6–16), y las nidadas incubadas por machos (12.6 ± 0.3 huevos) fueron significativamente más grandes que las incubadas por hembras (11.4 ± 0.4 huevos). La fecha promedio de eclosión para todos los nidos fue julio 2 (rango: junio 10–julio 23). Dos de las seis hembras cuyos nidos fueron depredados volvieron a nidificar. Las hembras apareadas produjeron un promedio de 24 huevos (rango: 20–28). La fecha promedio de eclosión para los machos apareados fue junio 30 \pm 3 días y para las hembras julio 3 \pm 3 días. El número promedio de días dedicados a actividades de nidificación estimado para las parejas que tuvieron éxito en la eclosión fue 59 (rango: 54–64). Las 12 hembras apareadas tuvieron éxito en la eclosión de al menos ocho pichones, contando ambas nidadas. Nuestros hallazgos indican que las nidadas simultáneas aseguran el éxito reproductivo de las hembras en *O. pictus* bajo condiciones que no serían favorables para otros modos de puesta de nidadas múltiples.

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INTRODUCTION

Various species of quail use monogamous or a combination of monogamous and polygamous mating systems to compensate for small body sizes, limited body reserves, fluctuating resources, and reduced sexual dimorphism (Brown and Gutiérrez 1980, Curtis et al. 1993, Burger et al. 1995). Monogamous and polygamous mating systems correspond to higher egg production per female compared to most promiscuous or polygynous upland gamebird species. Mountain Quail (*Oreortyx pictus*) are apparently monogamous and pairs participate in incubating simultaneous clutches and rearing simultaneous broods (Pope and Crawford 2001).

The secretive nature of Mountain Quail and the rugged, densely vegetated terrain that the birds inhabit are recognized as factors limiting the number of nesting studies (Gutiérrez and Delehanty 1999). Biparental brood rearing was reported and shared incubation postulated for Mountain Quail as early as the 1890s (Bendire 1892). Miller and Stebbins (1964) reported both sexes develop incubation patches, providing further evidence of biparental incubation. Heekin (1993) reported incubation by a male Mountain Quail in Idaho in 1992 followed by documentation in 1993 of successful nesting and brood rearing by a male in California (Delehanty 1995). Furthermore, the telemetry work conducted by Pope and Crawford (2001) found that Mountain Quail pairs closely associate throughout the nesting and brood-rearing periods.

Recent work by Delehanty (1997) and Pope and Crawford (2001) provide estimates for reproductive parameters such as clutch size, incubation length, and hatching date; however, Delehanty (1997) primarily studied captive birds. Pope and Crawford (2001) translocated quail from one wild population to another and then studied both populations simultaneously, thus potentially influencing factors related to reproduction, including densities and pair formation for resident and translocated populations. Here, we provide basic measures of productivity and reproductive chronology for wild Mountain Quail under normal density conditions.

We report nesting ecology and reproductive parameters for Mountain Quail relative to sex and age over four years. We also evaluate results from paired quail, which provide preliminary estimates of total female reproductive output as

well as male contribution to total female breeding success. Our objectives were to (1) compare reproductive parameters of clutch size and hatching date, estimate nest success and evaluate other important aspects of reproduction such as nest fate for second year (SY) and after second year (ASY) male and female Mountain Quail over four years, and (2) estimate breeding parameters including total egg production, initiation of egg laying, hatching date, and total time devoted to nesting; and to monitor other aspects of nesting ecology for paired Mountain Quail in order to evaluate female breeding success.

METHODS

STUDY AREA

Mountain Quail are found from the Baja Peninsula in Mexico, north to Vancouver Island in British Columbia, Canada, and east to west-central Idaho and northern Nevada (Gutiérrez and Delehanty 1999, Crawford 2000). Archaeological evidence suggests Mountain Quail are native to southern, central, and western Idaho (Gruhn 1961, Murphey 1991); however, populations have declined >90% over the past several decades and are primarily restricted to the Little Salmon River, small portions of the lower Salmon and Snake rivers, and the Boise River drainage (Brennan 1990, Vogel and Reese 1995, Crawford 2000). Declines are largely attributed to loss, degradation, and fragmentation of riverine and streamside shrub communities used by Mountain Quail as wintering habitat (Brennan 1990).

We studied Mountain Quail near Pollock, southwestern Idaho County, Idaho (45°17'N, 116°22'W), from 1992–1995. The study area encompassed nearly 22 km² along the Little Salmon River and tributaries and was based on surveys and recommendations from other studies. Elevations ranged from 716 to 1537 m with topography characterized by steep, dissected slopes with basaltic outcrops and ridges. Climatic data were obtained from a weather station in Riggins, Idaho situated at 549 m (Western Regional Climate Center 2005). Average temperatures from April through September were 19°C, 17°C, 19°C, and 17°C from 1992 to 1995, respectively (30-year [1971–2000] average = 19°C). April through September cumulative precipitation was 187 mm, 299 mm, 148 mm, and 300 mm from 1992 to 1995, respectively (30-year average = 228 mm; Western Regional Climate Center 2005).

Shrubs common in small draws and on mesic north-facing slopes were black hawthorn (*Crataegus douglasii*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), currant (*Ribes* spp.), mallow ninebark (*Physocarpus malvaceus*), and wild rose (*Rosa* spp.). Shrubs and trees common along stream bottoms and near springs and seeps included aspen (*Populus tremuloides*), blue elderberry (*Sambucus cerulea*), and red-osier dogwood (*Cornus sericea*). Saskatoon serviceberry (*Aamelanchier alnifolia*) was found on dry upland sites and oceanspray (*Holodiscus discolor*) and mallow ninebark commonly grew under conifer forest canopies. Black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) occurred along the Little Salmon River. Grasses inhabiting xeric, south-facing slopes included bluebunch wheatgrass (*Pseudoroegneria spicata*), cheatgrass (*Bromus tectorum*), Idaho fescue (*Festuca idahoensis*), and prairie junegrass (*Koeleria macrantha*). Ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) occupied mesic and higher elevation sites. Exotic weedy forbs such as knapweed (*Centaurea* spp.) and thistle (*Cirsium* spp.) had invaded some disturbed areas.

The majority of the study area was privately owned, with homesteads or small ranches situated in bottomlands and on flat benches above bottomlands. Smaller amounts of land were owned and managed by the Bureau of Land Management and U.S. Forest Service. Predominant land uses were livestock grazing and logging.

CAPTURE AND TELEMETRY MONITORING

We trapped Mountain Quail from mid-January through mid-March 1992–1995 in several intermittent drainages off the Little Salmon River. We also trapped birds from mid-August to mid-October in 1994. To trap quail, we used modified rectangular Stoddard quail traps (Shultz 1950, Gooden 1953, Smith et al. 1981) and circular traps placed under shrubs. All traps included soft, net tops to prevent injury to quail. Traps had one or two funnel openings, and were baited with a mixed grain and seed combination consisting of cracked corn, wheat screenings, Austrian pea screenings, black sunflower seeds, milo, and millet. For each captured bird, we recorded age, sex, and mass, and we fitted birds with an aluminum Idaho Department of Fish and

Game leg band. At the time of capture, we classified quail as SY or ASY based on plumage characteristics (Leopold 1939). Chicks captured in late summer and early fall 1994 were classified as hatching year birds. In 1992, we sexed quail based on hind-neck coloration (McLean 1930, Schlotthauer 1967), but this method was determined to be inaccurate in our area. After 1992, sex was determined genetically from blood extracted from the metatarsal vein (Longmire et al. 1993, Delehanty et al. 1995). We also used instances of male crowing, mating behavior, and necropsies to identify or confirm sex (Gutiérrez and Delehanty 1999).

During the first year of our study we preferentially attached radio-transmitters to females because we were unaware that male Mountain Quail contributed substantially to incubation and brood rearing. From 1993 to 1995 we selected quail of both sexes for radio-marking following the discovery in 1992 that male Mountain Quail contributed to incubation duties (Heekin 1993). We attached radio-transmitters to quail of all ages.

We equipped quail captured in 1992 with either a poncho-mounted, solar-powered radio-transmitter or a necklace-mounted, battery-powered radio-transmitter (Pyrah 1970, Amstrup 1980), and we equipped those captured from 1993 to 1995 with necklace-mounted transmitters. Combined weight of the radio-transmitter-poncho combination was 7.1 ± 1 g, approximately 3% of mean body weight, whereas the weight of the necklace-mounted radio-transmitter was approximately 3.7 g, or <2% of mean body weight.

We used radio-telemetry to locate birds on the ground once or twice per week from March to September to determine nesting chronology, locate nests, monitor incubating birds, and determine pair associations. Because our identification of pairings was based on associations detected through radio-telemetry and not confirmed with genetic analyses, we use the term “apparent monogamy” when referring to pairs of Mountain Quail (Burger et al. 1995). Consequently, when both pair members incubated clutches, we ascribed paternity of both clutches to the male. We identified nest locations by observing incubating radio-marked birds on nests or flushing incubating birds from nests. We did not mark nests to reduce disturbance and potential for predation. Universal Transverse Mercator

(UTM Zone 11; datum, NAD 1927) coordinates and elevations were recorded at each nest from USGS 1:24 000 topographical maps.

NESTING DATA

We counted the number of eggs in each clutch and subsequently checked nests through visual inspections and telemetry verifications on a regular basis to detect nest fate, confirm clutch size, and estimate hatching date. Following discovery of nests, average number of nest checks was ≤ 3 in 1992, 6.9 ± 1.2 in 1994, and 7.4 ± 0.7 in 1995. Time between nest checks averaged 4.0 ± 0.5 days in 1994 and 3.6 ± 0.2 days in 1995. Although not consistently recorded, number and regularity of nest checks in 1993 was similar to 1994 and 1995. Once incubating quail left nests for more than 24 hr, we revisited nests to confirm clutch size (count eggshell fragments, membranes, and remaining eggs) and determine nest and egg success. Purposeful nest checking near the projected hatching date of each nest allowed us to be able to reliably determine nest fate.

We report clutch size for first nests, where first nests are defined as a nest in which at least one egg was laid and we observed no earlier nesting attempt for that quail. We defined successful nests as nests in which at least one egg hatched. If a nest was unsuccessful, we determined its fate (Rearden 1951); we recorded nest fates as successful, depredated, infertile, or abandoned. We defined renests as a nesting attempt subsequent to an earlier unsuccessful nest attempt in which at least one egg was laid. We calculated egg success as the percent of hatched eggs per clutch. We measured female breeding success as the percent of females hatching at least one chick from their own nest or their mate's nest and thus calculated this only for known pairs of Mountain Quail.

Much uncertainty exists relative to Mountain Quail incubation lengths and egg-laying rates (Delehanty 1997, Gutiérrez and Delehanty 1999). Captive Mountain Quail may lay one egg per day for up to four days in succession, an adaptation that most likely shortens the overall time period needed to lay two clutches (Delehanty 1997); an egg-laying rate of 1.2 days per egg for wild Northern Bobwhite (*Colinus virginianus*, Klimstra and Roseberry 1975) suggests that quail are capable of rapid egg laying. Pope and Crawford (2001) reported a mean in-

cubation length for wild Mountain Quail of 30 days for males and females. We thus used an egg-laying rate of 1.2 days per egg with an incubation length of 30 days to calculate total combined days for egg laying and incubation. Our calculations were based on total egg production for paired females where both clutches were successful. Total egg production was multiplied by the number of days to lay an egg. This number was added to incubation length, then the sum subtracted from hatching date to estimate total days females spent in nesting activities.

STATISTICAL ANALYSES

Because we found each nest at the initiation of incubation and we were able to determine the fate for each nest, the apparent estimator of nest success (successful nests \times total nests⁻¹) provided unbiased estimates of nest success during incubation (Shaffer 2004). We computed the variance for each apparent nest-success estimate as the variance for a population proportion from a simple random sample (Scheaffer et al. 1996). To evaluate the influence of age, sex, and year on nest success of Mountain Quail during incubation, we used logistic regression to model nest success for 45 nests where we had identified incubators to age and sex using SAS statistical software (SAS Institute 2001, Shaffer 2004). Our global model included age, sex, age*sex, and year explanatory variables. We coded the response variable in our models as 1 for successful nests and 0 for failed nests. We evaluated the strength of evidence for each model with Akaike's information criterion for small samples (AIC_c). Differences between AIC_c for each model and the best model (Δ AIC_c) provided a ranking of models from the most to the least supported and Akaike weights (w_i) allowed us to assess the weight of evidence in favor of each model. We followed the convention that models with Δ AIC_c = 0–2 were competitive with the best model, and models with Δ AIC_c > 10 were poor-fitting models (Burnham and Anderson 2002). Rates of nest success during the 30-day incubation period were predicted from the parameter estimates for models best explaining nest success with the logistic function ($\exp[\beta_0 + \beta_1 x_1] / (1 + \exp[\beta_0 + \beta_1 x_1])^{-1}$) (Shaffer 2004). We report all estimates of nest success during incubation as percentages with 95% confidence intervals.

We used ANOVAs to evaluate differences in age, sex, year, and interactions, for clutch size, hatching date, and date of initiation of incubation. Nonsignificant interactions in ANOVA models were pooled into sampling error. Total egg production for paired females was evaluated using ANOVA, to examine differences between female age and among years in which each paired female was located. After finding no differences among years and between sexes with an ANOVA, we used a paired *t*-test to evaluate differences in hatching date between successful male and female pairs. We used a paired *t*-test to evaluate difference in elevation of nests for paired Mountain Quail. We used a one-tailed, one-sample *t*-test to evaluate whether mean distance between paired nests was greater than 200 m to provide a comparison to nests for six pairs of wild Mountain Quail in Oregon, which were found to all be <200 m apart (Pope and Crawford 2001). Statistical analyses were performed in SAS (SAS Institute 2001) with a significance level of $\alpha = 0.05$. All data are reported as means \pm SE.

RESULTS

We trapped 178 Mountain Quail from 1992 to 1995, of which 97 (54%) were female, 67 were male (38%), and 14 (8%) were not identified to sex. We fit 132 (74%) quail with radio-collars, of which 66 (50%) were female, 54 (41%) were male, and 12 (9%) were of unknown sex. Crowing and pairing generally increased in mid- to late March, with most pairs localized on breeding territories by early to mid-April. The earliest nest we observed was that of a SY male, believed to be associating with a SY female, found on 20 April 1992.

We located 52 first nests that contained a total of 612 eggs. Of these eggs, 431 (70%) hatched. Sex and age of incubating individual birds was found to be 10 ASY females, 17 SY females, 9 ASY males, 9 SY males, 2 females of unknown age, 1 male of unknown age, and four quail of unknown sex and age. Apparent nest success estimates during incubation were $\geq 50\%$ for each year and age*sex category (Table 1). Of the 52 nests, 11 were depredated (21%), one was infertile, and one was abandoned. Two of six females whose first nest was depredated re-nested and no birds produced consecutive broods. Thirty-one of 462 eggs (7%) in successful nests did not hatch.

TABLE 1. Apparent nest success and 95% CI (lower, upper) for the 30-day incubation period for Mountain Quail first nests by age and sex, and year categories, of birds breeding in west-central Idaho, 1992–1995.

Category	<i>n</i>	Percent nest success
Age and sex ^a		
After second year males	9	78 (44, 100)
After second year females	10	80 (50, 100)
Second year males	9	89 (63, 100)
Second year females	17	71 (47, 95)
Years		
1992	8	50 (5, 95)
1993	13	77 (50, 100)
1994	17	71 (47, 95)
1995	14	93 (78, 100)
All nests	52	75 (63, 87)

^a Nest success for quail of unknown age or sex are not reported, but are included in yearly and all nest estimates.

The best-supported models explaining nest success for 45 nests of known age and sex of incubator were the constant survival model or the model without explanatory variables, and the sex model (Table 2). Nest success based on the constant survival model was 78% (95% CI: 63–88), and nest success based on the sex model was 83% (95% CI: 59–95) for males and 74% (95% CI: 15–98) for females. An odds ratio computed with parameter estimates from the sex model indicated male-incubated nests were 1.7-times (95% CI: 0.4–7.9) more likely to be successful than female-incubated nests.

Mean clutch size for all first nests was 11.8 (range: 6–16). We found no difference in clutch size among years, between ages, or among year, age, and sex interactions for 48 birds of known sex. Clutches incubated by males ($n = 19$, 12.6 ± 0.3 eggs) were larger than clutches incubated by females ($n = 29$, 11.4 ± 0.4 eggs; $F_{1,41} = 4.9$, $P = 0.03$). Hatching date for 37 nests where sex of incubator was known differed among years ($F_{3,30} = 3.5$, $P = 0.03$) with mean hatching date significantly earlier in 1994 than in 1993 (Table 3). Mean hatching date for males was six days earlier than for females (Table 3), but we found no statistical difference between ages and sexes, or for age, sex, and year interactions for hatching date.

NESTING ECOLOGY OF QUAIL PAIRS

We identified three mated pairs of Mountain Quail in 1993, five in 1994, and four in 1995.

TABLE 2. Model selection results for nest success (S) of Mountain Quail ($n = 45$), breeding in west-central Idaho, 1992–1995. Models are listed according to the model that best fit the data and ranked by ΔAIC_c ; ΔAIC_c is the difference between the model with the lowest Akaike’s information criterion for small samples (AIC_c) and the AIC_c for the current model. The strength of evidence for each model is assessed with Akaike weights (w_i). Model fit is described with the value of the maximized log-likelihood function ($\log(L)$) and the number of parameters (k).

Model	$\log(L)$	k	ΔAIC_c^a	w_i
S _{CONSTANT}	-23.84	1	0.00	0.48
S _{SEX}	-23.56	2	1.64	0.21
S _{AGE}	-23.82	2	2.17	0.16
S _{YEAR}	-21.82	4	2.87	0.11
S _{AGE + SEX + AGE*SEX}	-23.21	4	5.65	0.03
S _{AGE + SEX + AGE*SEX + YEAR}	-21.35	7	9.96	0.00

^a The lowest AIC_c value was 49.77.

All pairs maintained apparent monogamous associations during egg laying and incubation. All mated pairs remained together following hatching and through brood rearing in August. In 1994, two nests of paired quail were depredated. One nest was incubated by a female of unknown age and an ASY male incubated the other nest. Consequently, we were unable to consider hatching date, initiation of incubation, and total time involved in egg laying and incubation for these two pairs in 1994 or for a pair in 1993 where the female incubated an infertile clutch. Mean distance between paired nests was 275 ± 65 m (range: 61–705) and did not differ from

200 m ($t_{11} = 1.1, P = 0.14$). There was no difference in elevation at paired nests, with males nesting on average at 1152 ± 61 m (range: 854–1513) and females at 1142 ± 46 m (range: 854–1336).

Twelve females produced an average of 24 ± 0.7 (range: 20–28) eggs in both clutches. We detected no differences in total egg production for year or age, or the year*age interaction for 11 females of known age. Total egg production for paired females was 284 eggs with 235 (83%) hatching. Of the hatched eggs, males hatched 54% and females hatched 46%. All 12 females hatched an average of 20 chicks (range: 8–26) from both clutches, corresponding to 100% breeding success. Hatching dates for males and females in nine pairs did not differ. Mean hatching date for males was 30 June \pm 3 days (range: 18 June–12 July) and for females was 3 July \pm 3 days (range: 22 June–22 July). On average, initiation of egg laying for nine paired females was 5 May \pm 4 days (range: 21 April–27 May), and initiation of incubation was 3 June \pm 3 days (range: 23 May–22 June). Our estimate of average time spent in egg laying and incubation for paired Mountain Quail was 59 days (range: 54–64 days) using an egg-laying rate of 1.2 days per egg.

TABLE 3. Hatching dates for first nests of Mountain Quail breeding in west-central Idaho, 1992–1995. Range in hatching dates for all nests was 10 June–23 July; nests incubated by males hatched from 10 June–19 July, and nests incubated by females hatched from 15 June–23 July.

Category	Nests	Hatching dates	
		Mean \pm SE (days)	Median
All nests	39	2 July \pm 2	29 June
1992	4	26 June \pm 4	25 June
1993	10	9 July \pm 3	11 July
1994	12	25 June \pm 3	25 June
1995	13	5 July \pm 3	4 July
Males	16	29 June \pm 2	29 June
1992	–	–	–
1993	5	5 July \pm 4	29 June
1994	6	22 June \pm 3	22 June
1995	5	1 July \pm 4	2 July
Females	21	5 July \pm 3	7 July
1992	2	2 July \pm 5	2 July
1993	5	12 July \pm 5	11 July
1994	6	28 June \pm 4	26 June
1995	8	8 July \pm 4	8 July

DISCUSSION

Male Mountain Quail contributed to female breeding success by incubating larger clutches, hatching more eggs, and achieving higher nest success. Each female Mountain Quail that was paired with an apparent monogamous mate was successful in achieving breeding success through her own clutch or through a simulta-

neous multiple clutch. Breeding-success benefits obtained from simultaneous multiple clutches requires that female Mountain Quail invest approximately two months in egg-laying and incubation activities. It is unclear why female Mountain Quail were less successful in nesting than males; however, energetic demands placed on females to lay an average of two-dozen eggs, may cause females to spend more time away from their nests foraging. Increased movements to and from nests to forage may lead to increased detection by nest predators.

In addition to laying two clutches simultaneously, other mechanisms female Mountain Quail could employ to optimize breeding success include sequential nests and broods, and renests. Guthery and Kuvlesky (1998) modeled the influence of sequential nests and broods on recruitment in Northern Bobwhite populations as indexed through autumn age ratios, and identified three variables crucial for high quail production: (1) the proportion of females participating in reproduction in a laying season, (2) the probability of nest success for any nesting attempt, and (3) the number of days in the laying season. With respect to these variables in light of findings from our study and those from Pope and Crawford (2001), (1) we assume the majority of SY and ASY female Mountain Quail engage in nesting activities, (2) nest success for Mountain Quail during incubation often exceeds 50%, and (3) sequential nests and broods seem unlikely in female Mountain Quail given constrained nesting seasons at higher elevations. Consequently, simultaneous multiple clutches should promote high productivity in Mountain Quail.

Renesting is common in other quail species such as Northern Bobwhite (Klimstra and Roseberry 1975, Burger et al. 1995), California Quail (*Callipepla californica*, Leopold 1977), and Scaled Quail (*C. squamata*, Schemnitz 1994), but is limited in Mountain Quail. In Oregon, one of nine (11%) female Mountain Quail whose nests were depredated renested (M. Pope, Oregon State University, pers. comm.). The only year we documented renesting was in 1994, the year with the driest breeding season. In addition, hatching dates were 16 days earlier in 1994, compared to 1993, a wet and cool year. It is possible that renesting in Mountain Quail is more common in years with mild climatic conditions, promoting earlier and longer nesting

seasons. Our weather comparisons are rudimentary and thus climatic effects on frequency of renesting in Mountain Quail needs further study.

Monogamous mating systems focus on defending a single mate, whereas polygamous mating systems occur when there are sufficient resources to monopolize several mates (Emlen and Oring 1977). In North American quail, male-biased sex ratios increase as sexual dimorphism increases, and these skewed ratios lead to increased intrasexual competition between males (Brown and Gutiérrez 1980). Increased sexual selection may lead males of some species such as California Quail and Northern Bobwhite to engage in incubation of simultaneous clutches, or as in Northern Bobwhite, to engage in a strategy where sequential polygyny and polyandry may occur together (Leopold 1977, Curtis et al. 1993, Burger et al. 1995). The mating system of Northern Bobwhite differs from multiple-clutch mating of Mountain Quail in that females incubate their first clutch, and then depending on the fate of this first nest, sometimes lay a clutch that is incubated by a male. While a male is incubating the second clutch, females sometimes lay and incubate a third clutch (Burger et al. 1995). In California Quail, multiple clutches appear to coincide with wet years when forage conditions are more favorable to high quail productivity (Leopold 1977).

Mean size of first clutches in Mountain Quail is 11–12 eggs, similar to Northern Bobwhite (Brennan 1999), and to California (Calkins et al. 1999), Gambel's (Brown et al. 1998), and Scaled Quails (Schemnitz 1994). Shorter nesting seasons and higher rates of nest success favor a nesting strategy of fewer, larger clutches (Farnsworth and Simons 2001). Concurrently laying two large clutches and simultaneously incubating them is a strategy that should optimize breeding success for birds inhabiting areas with short nesting seasons, as occurs in mountainous regions. Female Mountain Quail differ from other female North American quail in that they appear to have a limited ability to renest. Therefore, renesting does not appear to be a plausible mechanism to ensure breeding success following nest failures. Monogamy, simultaneous multiple clutches, and biparental care provide Mountain Quail with mechanisms to maximize reproduction in mountainous environments characterized by limited plant growing seasons and stochastic environmental conditions (Pope and Crawford

2001). These conditions likely preclude polygamous mating systems, and moreover laying simultaneous multiple clutches in monogamous Mountain Quail increases the likelihood of female breeding success.

Precipitous population declines in Mountain Quail east of the Cascade and Sierra Nevada Mountains prompted private conservation groups to file a petition to designate these birds as a threatened or endangered distinct population segment of the species under the Endangered Species Act, but this listing was denied (USDI Federal Register 2003). In Idaho, recovery of extensive areas of Mountain Quail habitat are not likely because over the past several decades livestock grazing, and hydroelectric and agricultural developments in riparian corridors have led to loss and degradation of shrubby riparian communities used by Mountain Quail for winter habitat (Brennan 1990, 1994). Recovery efforts in Idaho and other areas with impaired habitats should focus on enhancing existing habitat, and where possible through expanding habitat. Land management activities such as logging and livestock grazing in breeding habitats should be limited or carefully planned from early April to mid-July to avoid or reduce disturbance to nesting Mountain Quail during their extended nesting period.

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