

A FIELD STUDY OF ORNAMENTS, BODY SIZE, AND MATING BEHAVIOR OF THE GAMBEL'S QUAIL

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ABSTRACT.—Male Gambel's Quail (*Callipepla gambelii*) have strikingly ornate plumage. Yet, captive experiments indicate that removing multiple ornaments does not necessarily alter patterns of female mate choice or male-male competition. To test these unexpected results, I observed a wild population of banded quail for three seasons to determine ornamental and body size traits associated with pairing date and winners of male contests. I also documented mating behaviors (e.g., pairing date, mate fidelity, brood size). Consistent with captive studies, male mass, rather than ornate plumage, was the primary feature related to winners of male contests and early pairing. Heavier males paired earlier, regardless of age, but did not exhibit significantly larger ornaments. Adults of both sexes were heavier and paired earlier than yearlings. Early pairing also correlated positively with brood size, suggesting that heavy, early nesting birds experienced greater fitness. Mating behaviors were flexible across seasons. Social monogamy decreased from 83% in 1996 to 30% in 1998, while polygamy (sequential, long term pairings) increased, particularly among yearlings and adult males. Adult females were equally likely to exhibit social monogamy or polygamy each season. They also exhibited the highest frequency of early pairing and the greatest keel scores (a general measure of condition), suggesting their capacity for breeding was high. At least two adult females abandoned their first mate after hatching and re-paired, in an apparent attempt to double brood. Received 31 August 2002, accepted 28 February 2003.

The Gambel's Quail (*Callipepla gambelii*) is a highly sexually dimorphic game bird of the arid southwestern United States. Males exhibit multiple plumage ornaments, such as a long head plume, light and dark belly patches, and a rusty head patch (Johnsgard 1973). Contrary to prediction, tests of captive Gambel's Quail and other galliform birds indicate that many extravagant feather traits of males do not play a primary role during female choice (Beani and Dessi-Fulgheri 1995, Buchholz 1995, Ligon and Zwartjes 1995, Hagelin and Ligon 2001, but see Calkins and Burley 2003) or male-male competition (Ligon et al. 1990, Buchholz 1997, Hagelin 2001a). Even the removal of multiple ornaments in Gambel's Quail and Red Junglefowl (*Gallus gallus*) did not alter patterns of female preference (Ligon and Zwartjes 1995, Hagelin and Ligon 2001). Instead, body size and testosterone-mediated traits often are favored and may function as reliable signals of male quality or condition (Ligon and Zwartjes 1995; Berglund et al. 1996; Hagelin 2001a, 2001b; Hagelin and Ligon 2001).

The principal goal of this study was to test

laboratory findings by studying Gambel's Quail in the field. Wild populations typically are male biased (Brown and Gutiérrez 1980), suggesting that ornaments may signal information to discriminating females or male competitors. I aimed to determine the ornamental and body size traits associated with (1) early pairing, which I found to be positively related to reproductive success, and (2) the winners of male contests. I observed a population of banded, free-ranging Gambel's Quail for three seasons (1996–1998) and recorded when mates paired and the outcome of aggressive interactions between males. I predicted that if male ornaments functioned during sexual selection, ornament size would correlate positively with early pairing or male status (Senar and Camerino 1998, Wolfenbarger 1999).

A second goal of the study was to characterize the mating behavior of Gambel's Quail. Though generally considered socially monogamous (Johnsgard 1973), at least one account suggests that double brooding may occur (Gullion 1956). Recent studies have documented multiple broods in other North American quail, and breeding strategies appear to be more flexible than previously surmised (Curtis et al. 1993, Burger et al. 1995, Delehanty 1995, Guthery and Kuvlesky 1998).

To assess mating behavior, I determined (1) the proportion of socially monogamous versus

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polygamous pairs in the population, (2) the sex and age classes of birds that exhibited different breeding strategies, and (3) how mating strategies changed across years. Climatic parameters, such as temperature and rainfall, are thought to influence the fluctuations of quail populations (e.g., Raitt and Ohmart 1967, 1968; Campbell 1968; Heffelfinger et al. 1999; Guthery et al. 2001; Lusk et al. 2001). However, the underlying breeding patterns of different sex and age classes are not well understood.

STUDY AREA AND METHODS

A field assistant and I monitored quail from January 1996 to August 1998 at Bosque del Apache (BDA) National Wildlife Refuge, San Antonio, New Mexico (34° 49' N, 106° 53' W). Quail commonly are seen foraging, sunbathing, and drinking within 10 m of a 3-m × 3-m observation window at the BDA visitor's center throughout the year. The habitat consists of open sandy soil interspersed with dense shrubs (four-winged saltbush, *Artemisia tridentata*). Refuge staff provided quail and other wintering birds with approximately 1 kg of wild bird feed (millet, cracked corn, milo, sunflower seeds) daily between December and February.

Trapping and measurements.—We trapped quail near the visitor's center from December to February using funnel traps baited with seed. Each bird received a unique combination of plastic color leg bands. We determined sex from the presence of ornate plumage and age (yearling or adult) from primary wing coverts (Brown et al. 1998). Measures of body size followed Hagelin and Ligon (2001) and included mass and length of tarsus, flattened wing, tail, and culmen. We also palpated the sternal keel (Gregory and Robins 1998) to obtain a general measure of body condition (fat and muscle). We categorized a bird's keel as: 0 (no fat or muscle; sharp keel), 1 (some fat and muscle; moderately sharp keel), or 2 (high fat and muscle; dull keel). Ornament measurements also followed Hagelin and Ligon (2001). Briefly, we measured the flattened plume length of both sexes. We also calculated the area (in mm²) of ornaments unique to males (light and dark belly patches, rusty head patch) by multiplying patch width and height. We measured rusty head patch in 1997 and

1998 only. We calculated mean trait sizes for birds that were trapped and measured more than once. All quail handling was conducted under Animal Welfare Assurance #A4023-01 and Univ. of New Mexico Animal Care Protocol #9801-B.

Pairing, brood size and hatching date.—Using binoculars, we monitored quail from the BDA observation window from March through mid-August. Observations usually occurred on alternate weeks during hours of peak activity (dawn until late morning, late afternoon until dusk). An observation period typically spanned two consecutive days and totaled 10–30 h of monitoring. An individual was considered paired when it was seen for ≥2 weeks (≥2 observation periods) in close proximity to the same individual of the opposite sex. The behavior of pairs was discernable from unpaired birds; pairs typically distanced themselves from others, followed each other while foraging, and the male usually chased off all other quail. We used only those birds that exhibited obvious changes in pairing status (e.g., unpaired before but consistently seen with mate after 23 April) in analyses of pairing behavior.

We recorded the number and age of chicks that accompanied banded birds. Chick age was estimated in 1-week increments. Raitt (1961) described plumage-based age estimates for California Quail (*C. californica*), which are virtually identical to Gambel's Quail (Raitt and Ohmart 1967). We estimated each brood's hatching date by subtracting the age of a brood (in weeks) from the date we observed it. To determine the median hatching date of the population more accurately, we also included data for unbanded parents with newly hatched broods (<1 week old). We distinguished between new broods during each observation period by the number of young. We avoided problems of duplicate counting, because observation periods took place every other week. Newly hatched chicks of unbanded birds grew markedly between these periods and were not counted again.

Male contests and mating behavior.—Male aggression was common during each season. We noted the band combination, the pairing status of each (whenever possible), and the outcome of encounters between pairs of banded males. "Winning" males caused their op-

ponents to retreat from the immediate area. "Losing" males either retreated immediately, or fled when an opponent escalated aggression.

We recorded the mating behavior of banded birds during pairing and breeding (March through mid-August). Individuals remaining with the same mate throughout this period were considered socially monogamous. In contrast, a bird seen with a partner for ≤ 2 weeks (approximately the time required to lay a clutch; Gorsuch 1934, Johnsgard 1973), that next associated with another mate for ≤ 2 weeks, was considered polygamous. We scored polygamy only when we saw both members of the original pair, as to exclude the possibility of mate mortality. We also noted extrapair behavior for birds that partnered with a new mate for one observation period, but had returned to their original, long term mate by the next period. Finally, we recorded breeding and parenting behaviors, including single parents with broods and multiple parents with communal broods.

Statistical analysis.—I calculated the age and sex ratios of the population annually. Differences in trait size between the sexes and age classes (yearling, adult) were assessed with 2-tailed *t*-tests, whereas differences in trait sizes across years were analyzed with ANOVA. Data were tested for normality prior to any parametric test. I used 2-tailed Fisher's exact tests to assess patterns related to keel scores.

I calculated the median pairing date for the population each season. I tallied the number of adults and yearlings that paired before, versus after, the median date and analyzed patterns with Fisher's exact tests. I used chi-square goodness of fit tests to assess age-assortative mating when both members of a pair were banded. MANOVA determined any significant differences in ornaments or body size relative to pairing date, age class, or across the three years studied. Separate MANOVA analyses were conducted for males and females, and each bird was used only once in each data set. Trait sizes were the dependent variables in each MANOVA analysis, whereas pairing date, age and year were independent, categorical variables. Pairing date compared traits of individuals that paired before versus

after the median pairing date, and age compared traits between yearlings and adults.

Stepwise discriminant analysis selected the specific traits that best described each significant categorical variable (pairing date, age, or year) from MANOVA analysis. These traits subsequently were analyzed with ANOVA and 2-tailed *t*-tests to determine how they varied relative to categorical variables. Since the rusty head patch of males was measured only in 1997 and 1998, an additional MANOVA model that included the rusty patch was run for males from these two years only. I also used Pearson correlations to clarify the relationship(s) between male ornaments and body size.

I determined the median hatching date annually and estimated the mean size of broods that hatched relative to the median date. Mean brood size was calculated in two ways: brood size of chicks ≤ 1 week old, and brood size pooled across all other chick ages. I used brood size of newly hatched chicks to estimate clutch size and hatching success, whereas data pooled across ages was used to estimate mean brood size during chick rearing. I tested the relationship between hatch date and brood size with 1-tailed *t*-tests, as late hatching broods typically are smaller (Price et al. 1988). I also compared mean brood size of adult and yearling pairs. Broods of banded birds were not observed frequently enough to determine the total number of young fledged. Therefore, seasonal changes in brood size (see above) were essential to understanding whether early pairing birds also experienced greater reproductive success. This approach was reasonable only if the pairing date of a bird correlated with the hatching date of its brood. That is, birds pairing before the median pairing date also should hatch broods before the median date and *vice versa*. Significance of the association between pairing and hatching was evaluated with a chi-square contingency table.

I used binomial and chi-square tests to determine if winning a contest was related to a male's age class or pairing status (paired versus unpaired). I subtracted ornamental and body size traits of the losing male from the winner to understand how traits related to winning. Winner-minus-loser ($W - L$) scores were analyzed with Wilcoxon signed rank

TABLE 1. MANOVA and discriminant analysis of Gambel's Quail breeding at Bosque del Apache, New Mexico, indicated that the significant effect of pairing date in males between 1996 and 1998 was best described by differences in mass and not ornaments. The significant effects of year and age were based on differences in ornaments (males) and body size (males and females).

Sex	Effect	F	df	P	Discriminant analysis ^a	F	P
Males	Pairing date	2.0	8, 141	0.0506	Mass	9.1	0.0030
	Year	12.4	8, 142	0.0001	Tarsus, tail, dark patch, white patch	14.9	0.0001
	Age	4.6	8, 141	0.0001	Mass, wing, culmen, plume	12.7	0.0001
Females	Pairing date	1.4	6, 101	0.1996	—	—	—
	Year	3.1	6, 102	0.0070	Tarsus, tail	9.0	0.0002
	Age	2.9	6, 101	0.0119	Mass, wing, tail	10.3	0.0001

^a Variables included mass (g); length (mm) of tarsus, culmen, tail, flattened wing, and flattened head plume; and area (mm²) of dark and white belly patches.

tests. Each pair of males used in signed rank tests was unique; therefore, $W - L$ scores represented independent data points. When male pairs interacted more than once, the bird that dominated a simple majority of contests was considered the winner, and only one $W - L$ score was included in the data set. Ornaments might operate differently over the course of the breeding season. For example, early contests that occur during pair formation may differ from late season contests that involve mate or chick guarding. Since the pairing status of males was not always known, I conducted signed rank tests on $W - L$ data sets collected before versus after the median pairing date. Given the large number of male traits used in signed rank tests, the risk of Type I error was high, which could have caused some variables to be significant by chance (Rice 1989). Therefore, I analyzed the entire $W - L$ data set simultaneously in a multiple logistic regression with a stepwise selection procedure. The analysis identified traits that best described winning males.

Finally, I determined the number of birds that were socially monogamous versus polygamous each season. I assessed any significant shifts away from social monogamy over the three year period with chi-square contingency tables and two-tailed Fisher's exact tests. Binomial tests analyzed patterns of monogamy: polygamy within each year, as compared to the 50:50 null expectation. I also used a contingency table and Fisher's exact test to determine whether adult or yearling pairs were more likely to act monogamously or polygamously.

RESULTS

Pairing.—We made 618 hours of behavioral observations over three seasons and recorded pairing status for 313 of 450 banded adults and yearlings. Median pairing dates occurred on 14 April (1996), 11 April (1997) and 4 April (1998). Contrary to predictions of ornament size, MANOVA analysis identified the mass of males as the only trait of either sex that correlated significantly with pairing date (Table 1). Regardless of year or age class, heavier males paired before the median pairing date (mean mass of adults before median: 184.5 g, after: 178.5 g, $t_{66} = 3.04$, $P = 0.003$; yearling males before median: 185.5 g, after: 174.5 g, $t_{89} = 3.89$, $P = 0.0002$). MANOVA also identified other traits of both sexes that varied significantly relative to year and age class (Table 1). These are considered separately, below (see Differences between years, age classes, and sexes). Interaction terms (e.g., year \times pairing date) were not significant. Results did not differ when data included rusty head patch. Male mass exhibited a weak positive correlation only with dark patch area ($r^2 = 0.025$, $P = 0.056$, $n = 162$; all other ornaments $r^2 \leq 0.0009$, $P \geq 0.70$). Weak correlations between other body size traits and ornaments also were positive ($0.026 \leq r^2 \leq 0.063$, $108 \leq n \leq 170$, $0.001 \leq P \leq 0.095$).

Adults of both sexes were more likely to pair before the median date (66% of 136 adults versus 43% of 177 yearlings, $\chi^2_1 = 15.9$, $P < 0.0001$). This pattern was more marked in adult females (75% of 57 paired early) than adult males (60% of 79, $\chi^2_1 = 3.7$,

TABLE 2. Gambel's Quail broods hatching before the median hatching date were larger than those hatched later in the season at Bosque del Apache, New Mexico. Two ages categories are given: newly hatched chicks (≤ 1 week) and broods of all other age classes (2–6 weeks). Significance is one tailed, as brood size was expected to decline for late hatching birds.

Year	Brood type	n	Mean brood size \pm SE		t	P
			Early broods	Late broods		
1996	≤ 1 week	28	11 \pm 0.6	6 \pm 0.9	2.5	0.020
	All ages	35	10 \pm 0.9	5 \pm 0.5	3.3	0.002
1997	≤ 1 week	31	12 \pm 0.9	8 \pm 1.0	1.8	0.080
	All ages	78	11 \pm 0.7	7 \pm 0.6	2.8	0.007
1998	≤ 1 week	11	12 \pm 1.2	5 \pm 0.9	3.2	0.010
	All ages	29	9 \pm 0.9	4 \pm 0.4	3.2	0.003

$P = 0.054$). Yearling birds showed no such pattern; exactly 43% of females ($n = 83$) and 43% of males ($n = 94$) paired before the median. Of 35 pairs in which both individuals were banded, 26 were the same age (18 adult pairs, 8 yearling pairs), while 9 were of mixed age ($\chi^2_1 = 8.1$, $P = 0.004$). In only four cases, pairs from a previous season mated again the following year; these birds always paired before the median pairing date. No birds paired with the same partner during all three years. Mortality probably inhibited pair bonds >2 years, as we noted it only three times.

Since age was related to pairing and some ornaments correlated with male size, I used multivariate ANCOVA to determine if early pairing males had ornaments that were larger than expected for their body size. For each age class, I regressed male ornaments against two predictor variables: (1) PRIN1 scores from a principle components analysis that described variation in male body size (mass, tarsus, wing, tail), and (2) pairing date, which denoted whether a male had paired before or after the median pairing date. Body size (PRIN1) correlated with significant differences in ornament size, but pairing date did not (adults: PRIN1: $F_{4,33} = 5.08$, $P = 0.003$, pairing date: $P = 0.70$; yearlings: PRIN1: $F_{4,61} = 3.45$, $P = 0.013$, pairing date: $P = 0.30$). Therefore, males pairing before versus after the median date did not differ significantly in ornament size, once body size had been taken into account.

Brood size and hatching.—We recorded the pairing date and estimated the hatching date for 100 birds with broods. Pairing date correlated positively with hatching date in 83 cases ($\chi^2_1 = 43.6$, $P < 0.0001$). Namely, birds

pairing before the median pairing date also produced offspring before the median hatching date and *vice versa*. The pattern did not differ significantly between the sexes ($P \geq 0.50$). Median hatching dates fell between 6 June (1996) and 11 June (1998). Broods that hatched before the median date were almost twice as large as those hatched later (Table 2). Adults and yearlings produced similar-sized broods (mean size pooled across all ages of chicks: adults: $n = 53$, mean = 8.0 chicks \pm 0.7 SE; yearling: $n = 42$, 8.0 chicks \pm 0.8 SE). We observed 15 single parents (nine male, six female) tending broods. In five instances (three female, two male), foster parenting apparently occurred, in which a single parent and brood associated with a new mate, and remained together during and following chick rearing. Broods also merged. In five cases, 3–5 parents tended excessively large numbers of chicks (mean brood size = 30 chicks \pm 7 SE).

Male contests.—We observed 110 aggressive encounters between different pairs of banded males. Mated males won contests against unpaired opponents 29:4 (binomial test, $P < 0.0001$), and adults tended to dominate yearlings 36:22 ($\chi^2_1 = 3.6$, $P = 0.056$). When both males were paired but differed in age, either male was likely to win (18:17).

Winning males were larger than losers with respect to mass (mean W – L score: 4.7 g, $w = 1210$, $n = 103$, $P < 0.0001$). No ornaments correlated with winning ($P \geq 0.50$). I obtained a similar pattern relative to the median pairing date (mean W – L score pre-median: 3.8 g, post-median: 5.1 g; $200 \leq w \leq 556$, $0.008 \leq P \leq 0.020$, $33 \leq n \leq 70$; all ornaments $P \geq 0.30$). Stepwise logistic analysis also selected

mass as the primary variable that accounted for the differences between winners and losers ($-2\log L\chi^2_1$ estimate: 12.8, $P < 0.001$).

Mating behavior.—Of 164 birds followed during breeding, 56% were socially monogamous and 44% were polygamous. Social monogamy in the population declined from 83% in 1996 to 30% in 1998, while polygamy increased ($\chi^2_2 = 31.5$, $P < 0.0001$). Significant shifts away from monogamy occurred in both sexes of yearling birds (males: Fisher's exact $P = 0.004$; females: $P = 0.001$; Fig. 1A, B) and adult males ($P = 0.001$; Fig. 1C). Adult females, however, were equally likely to exhibit social monogamy or polygamy each year ($P = 0.90$; Fig. 1D). Adult males exhibited a higher frequency of social monogamy (mean = 67%; Fig. 1C), compared to yearlings (51%; Fisher's exact $P = 0.028$; Fig. 1A, B). Pairs of adults tended to be more monogamous (50% of 26) than paired yearlings (27% of 37; Fisher's exact $P = 0.062$). The polygamous behavior of adult females (Fig. 1D) tended to differ from all other members of the population combined (Fig. 1A–C; Fisher's exact $P = 0.061$). We excluded 23 birds from analyses that appeared to act polygamously, but for which we could not exclude the possibility of mate mortality.

A majority of socially monogamous birds (59%) exhibited at least one short (<2-week) extrapair bond. All returned to and tended any chicks with their original mate. Most polygamous birds (78%) exhibited long term, sequential pairings. For example, a banded pair, male blue-left (BL) and female yellow-right (YR), remained together between 4 April and 13 May. By 31 May, BL associated with another female and remained with this mate through the end of the breeding season. YR also paired with another male. Polygamous birds typically switched mates one to two times during a season (e.g., in May and again in June or July). Two adult females in 1996 abandoned their mates and 5- to 6-week-old broods and re-paired with new partners. Three pairs that separated early in the season (May), and had acquired new mates, reunited again later in July. Two reunited pairs were tending a brood.

Differences between years, age classes, and sexes.—Both year and age were significant effects in the MANOVA model (Table 1). Dis-

criminant analysis indicated that the size of ornamental patches of males varied significantly among years, but not between age classes (Tables 1, 3). Two body size traits of both sexes (tarsus, tail length) also varied among years (Table 1). Both decreased slightly over the study period (mean tarsus of both sexes, 1996: 32.1 mm, 1997: 31.2 mm, 1998: 30.8 mm; $F_{2,448} = 38.1$, $P < 0.0001$; mean tail, 1996: 100.2 mm, 1997: 99.0 mm, 1998: 97.5 mm; $F_{2,444} = 5.0$, $P = 0.001$).

Discriminant analysis distinguished between age classes of both sexes on the basis of body size (mass, wing, tail, culmen; Table 1). Adults were larger than yearling birds (mean mass, adult male: 182.4 g, yearling: 176.7 g, $t_{244} = 3.18$, $P = 0.002$; adult female: 179.8 g, yearling: 172.4 g, $t_{201} = 2.97$, $P = 0.003$; wing, tail, culmen: $199 \leq n \leq 249$, $2.3 \leq t \leq 3.4$, $0.0008 \leq P \leq 0.007$). Length of head plumes varied relative to age class in males only (Table 3). Surprisingly, plumes of adult males were slightly, but consistently, shorter than yearling males (Table 3; mean adult: 40.9 mm, yearling: 42.1 mm; $t_{246} = 3.18$, $P = 0.002$).

Males were somewhat larger than females, regardless of age (mean mass, male: 178.8 g, female: 173.0 g, $t_{447} = 3.0$, $P = 0.003$; wing, male: 117.6 mm, female: 115.4 mm, $t_{448} = 8.27$, $P < 0.0001$; tarsus, male: 31.7 mm, female: 30.8 mm, $t_{448} = 7.46$, $P < 0.0001$; tail, male: 101.0 mm, female: 96.1 mm, $t_{444} = 6.87$, $P < 0.0001$; culmen, male: 11.4 mm, female: 11.2 mm, $t_{446} = 2.89$, $P = 0.004$; plume: male: 41.7 mm, female: 31.3 mm, $t_{446} = 46.17$, $P < 0.0001$). We palpated the keel of 163 quail. Ten of 18 adult females obtained the highest score, indicating they had the greatest amount of muscle and fat on their breasts, compared to only 26% of all other birds (Fisher's exact $P = 0.014$).

Population changes.—The 450 Gambel's Quail trapped at BDA exhibited a male-biased sex ratio, due to a scarcity of adult females each year and an over abundance of yearling males in 1998 (Table 4). The age distribution of the population also shifted. In 1996, yearlings were approximately 20% more common than adults, but by 1998, they were 50% more common (Table 4). The resulting 30% increase in the relative abundance of yearling

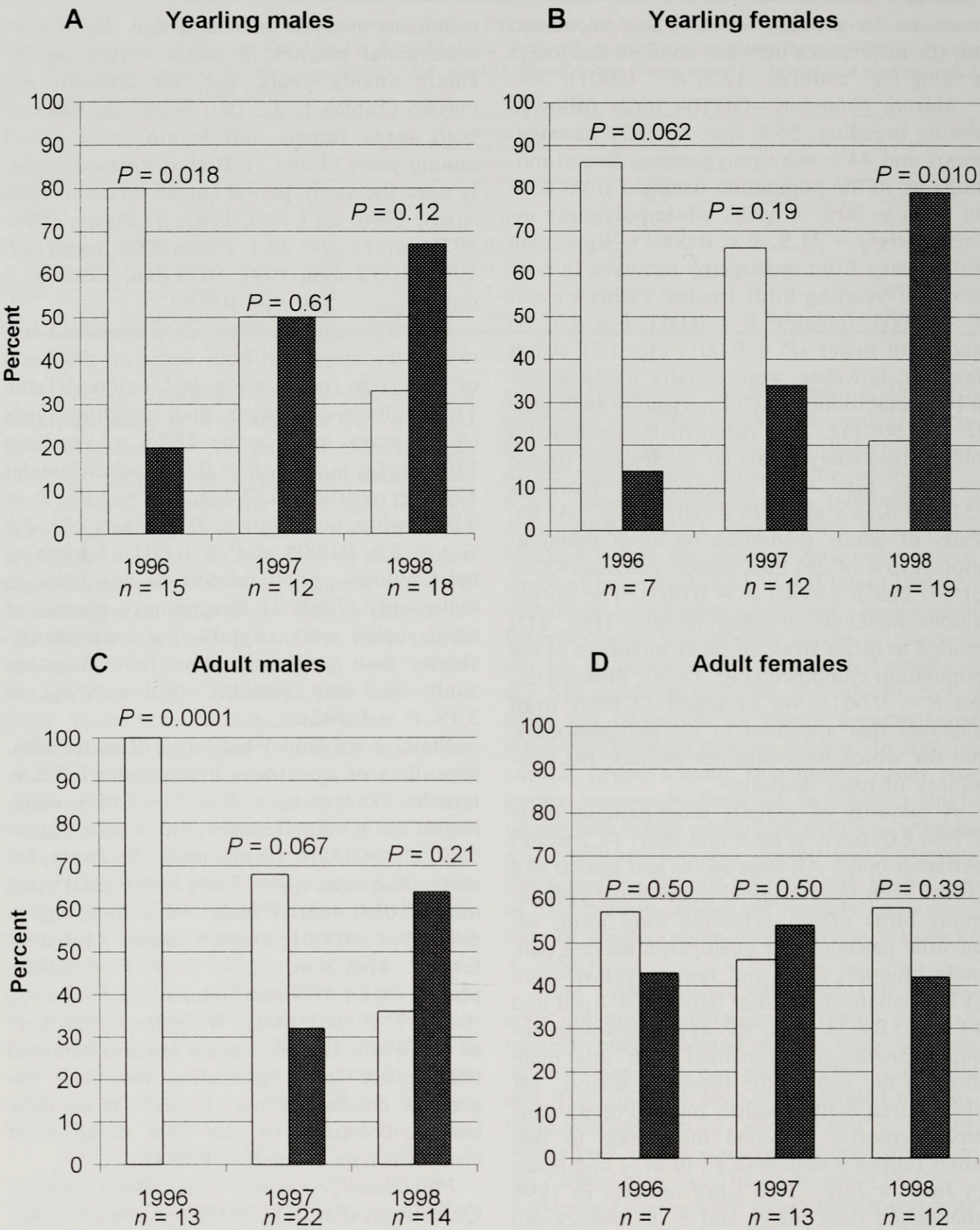


Fig. 1. Significant shifts away from monogamy occurred across years for all groups of Gambel's Quail at Bosque del Apache, New Mexico, except adult females: (A) yearling males, Fisher's exact $P = 0.001$; (B) yearling females, $P = 0.001$; (C) adult males, $P = 0.001$; and (D) adult females, $P = 0.90$. Open bars are monogamous individuals, solid bars are polygamous individuals. Patterns within each year were compared to the null expectation of 50:50 (monogamy : polygamy); the cumulative binomial probability $P(x \geq k)$ for each is given above the bars.

TABLE 3. Ornament sizes of male Gambel's Quail at Bosque del Apache, New Mexico, varied by year and by age class between 1996 and 1998. Contrary to prediction, adult males did not have larger ornaments than yearlings. Significant differences across years or between age classes are indicated in the Trait and Age columns, respectively. Rusty head area was not measured in 1996.

Trait	Age	1996 (n = 66)	1997 (n = 82)	1998 (n = 100)
Dark patch area (mm ²)**	Yearling	1407.4	1111.0	1356.7
	Adult	1431.2	1092.8	1636.8
White patch area (mm ²)**	Yearling	1990.7	1482.9	1738.3
	Adult	1977.9	1478.1	1881.9
Rusty head area (mm ²)*	First-year	—	489.1	514.8
	Adult	—	487.7	527.6
Plume (mm)	Yearling**	42.5	43.0	41.5
	Adult	41.5	41.0	39.5

* $P = 0.05$, ** $P = 0.001$.

birds was significant ($n = 450$, $\chi^2_2 = 8.3$, $P = 0.016$).

DISCUSSION

Ornamental versus body size traits.—Field observations of Gambel's Quail were consistent with the results of captive experiments. Instead of ornaments, male body size, specifically mass (Table 1), was the primary trait that correlated with early pairing and winners of male contests. In captive tests, the body size traits and behavior rates of males were primarily related to female preferences and the winners of male contests, whereas natural variation of single ornaments and experimental removal of multiple ornaments was not (Hagelin 2001a, 2001b; Hagelin and Ligon 2001).

Heavier (and older) males at our field site also were the best competitors. Mass was the primary trait related to winning early season contests and the only trait that varied significantly relative to pairing date (Table 1), indicating that mass (or male size) may influence mate acquisition. In the related California Quail, only those birds that belonged to a male

dominance hierarchy were successful in obtaining a mate (Mastrup 1987).

Unlike mass, male ornaments varied significantly among years and between age classes (Tables 1, 3). Flexibility of ornament size suggests that ornaments potentially could serve as indicator traits during some years. Yet, patches were not predictably larger (or smaller) in adults (Table 3), and all ornaments exhibited rather weak correlations with mass and body size traits. Although early pairing males were heavier (Table 1), discriminant and ANCOVA analyses indicated they did not exhibit significantly larger ornaments than other birds in the population. Early pairing, however, resulted in larger broods (Table 3), suggesting that heavier males experienced greater success, regardless of ornament size. Interaction terms of the MANOVA model (e.g., year \times pairing date) also were not significant, indicating the relationship between ornaments and pairing date did not change from year to year. The failure to detect any significant pattern of ornaments relative to pairing date (Table 1) did not result from a general lack of statistical

TABLE 4. Yearling and adult Gambel's Quail trapped at Bosque del Apache, New Mexico, exhibited a male-biased sex ratio (% males), a scarcity of adult females, and an increase in the relative abundance of yearlings between 1996 and 1998.

Age	Males (n)			Females (n)			% Males (%)			Age distribution (%)		
	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998
Yearling	35	53	75	35	52	63	50.0	50.4	54.3	59.8	70.0	75.4
Adult	31	29	25	16	16	20	66.0	64.4	55.6	40.2	30.0	24.6
Total	66	82	100	51	68	83	56.4	54.6	54.6	100.0	100.0	100.0

power. Samples were capable of detecting intermediate and large effects of ornament size relative to pairing date, while retaining 80% statistical power (Cohen 1988). Understanding smaller effects of ornaments will require larger samples or perhaps the use of composite indices to enhance the combined effect of multiple ornaments (Calkins and Burley 2003).

In previous captive manipulations (Hagelin 2001a), only one ornate trait, the head plume of Gambel's males, affected the outcome of aggressive contests. Hagelin (2001a) suggested that plume position (erect versus flattened) affected contests, rather than differences in plume length. Field observations confirmed lab findings. Natural variation in plume size did not correlate with winning or early pairing. Adult males, which were larger and usually dominated yearling males, actually had slightly (but significantly) shorter plumes (5% or 1–2 mm; Table 3). Any social benefit of slightly longer plumes appeared to be minimal for yearlings. They were unlikely to win contests or pair early, regardless of plume size.

Several investigations of ornately-feathered species within the order Galliformes have reported similar, and equally counter-intuitive results to those of Gambel's Quail. Specifically, a strong relationship frequently is lacking between the ornate plumage of males and breeding behavior in species such as the Red Junglefowl (*Gallus gallus*; Ligon et al. 1990, Ligon and Zwartjes 1995), Wild Turkey (*Meleagris gallopavo*; Buchholz 1995, 1997), and Grey Partridge (*Perdix perdix*; Beani and Desi-Fulgheri 1995). Even the simultaneous removal of multiple ornaments did not alter patterns of female preference (Ligon and Zwartjes 1995, Hagelin and Ligon 2001). Rather than a direct involvement of ornaments in sexual selection, many traits appear to have lost their key signaling function and, instead, may be maintained through alternative mechanisms, such as weak selection (Möller and Pomiankowski 1993, Hagelin and Ligon 2001). It is unclear, however, how weak sexual selection must be in order to maintain ornaments. Our data revealed a poor correlation between body size and ornate traits, which may be a sufficient mechanism for ornament maintenance.

If certain plumage ornaments do not reflect

male quality, sexual selection may operate on other, more reliable traits (Kodric-Brown and Brown 1984, Möller and Pomiankowski 1993, Hill 1994). Body size generally is thought of as an honest signal, because it is related to an underlying quality that cannot be faked (Maynard Smith and Harper 1988, Guilford and Dawkins 1995, Taylor et al. 2000). Body size of wild quail was clearly linked to age, size, early pairing in both sexes (see also Mastrup 1987), and to male status. Given that Gambel's Quail do not usually live beyond their first breeding season (Sowls 1960), both size and age appear to honestly indicate an individual's overall breeding quality. Experiments using captive quail were consistent with these results; females typically preferred larger males and larger males also won male contests (Hagelin 2001a, Hagelin and Ligon 2001). High keel scores (greater fat and breast muscle) were also associated with age and large size of wild adult females, which may reflect a greater potential for reproduction (Reynolds 1997).

Rather than assessing each ornament separately, Calkins and Burley (2003) considered "composite traits" by combining multiple ornaments of California Quail in analyses of female choice. The exact role, if any, of composite traits in Gambel's Quail is presently unclear. Manipulations that removed both single and multiple ornaments from captive yearling males did not alter mating preferences of females (Hagelin and Ligon 2001). Ligon and Zwartjes (1995) have reported similar results for Red Junglefowl.

Mating behavior.—Gambel's Quail exhibited a flexible breeding strategy which changed markedly from 83% monogamy in 1996 to 70% polygamy in 1998. The resulting 53% increase in polygamy within the population was due to two factors. First, the frequency of polygamy increased in yearling birds and adult males between 1996 and 1998 (Fig. 1A–C). Second, the relative abundance of yearlings increased by 30% over three years (Table 4), and yearling pairs were more likely to exhibit polygamy than adults.

Although the proximate cues underlying individual breeding behavior are unknown, the environmental conditions that influence the disruptive nature of semi-arid quail populations (Forrester et al. 1998, Heffelfinger et al. 1999,

Guthery et al. 2001) appear to provide a mechanism. Extreme heat or lack of precipitation, for example, can influence brood failure (Heffelfinger et al. 1999, Guthery et al. 2001), thereby increasing the frequency of re-pairing. High levels of polygamy at our study site (1998; Fig. 1A–C) coincided with a ten-year low in rainfall at the time of hatching (June), whereas high levels of monogamy (1996; Fig. 1A–C), corresponded to a 25-year high.

Mean mass of both sexes at Bosque del Apache was within the range reported for other wild populations (160–200 g; Brown et al. 1998), suggesting that birds were not abnormally fattened by supplemental winter feed. However, feed could have created a high local nesting density, thereby enhancing re-pairing opportunities relative to other breeding sites. Though absolute measures may differ, the relative changes I observed in brood size (Table 2) and in the breeding behavior of individuals (Fig. 1A–C) occurred independently of winter feed, which remained constant throughout the study.

Adult males, the largest, most dominant birds in the population, exhibited the highest frequency of social monogamy (Fig. 1A–D), indicating monogamous behavior was a preferred breeding strategy. Male California Quail also exhibited an unwillingness to behave polygamously, even during manipulations of sex ratio (see Lott and Mastrup unpubl. data in Calkins et al. 1999). Our data provide several insights into why social monogamy may be favorable. First, pairing date and age-assortative mating indicated that adult males had a good chance of obtaining a quality mate (a large adult female) early on. Heavier adults that paired early had a high likelihood of successful breeding (Table 2), and some adult females attempted second broods. Were a male to abandon its first mate and re-pair, it would be difficult to obtain another mate, particularly an adult female, given their scarcity in the population (Table 4).

Adult females consistently maintained a mean frequency of 46% polygamy, regardless of year (Fig. 1D). This pattern was unlike the more variable breeding behavior of other members of the population (Fig. 1A–C). Adult females also had the highest keel scores and were more likely to pair before the median

pairing date than any other birds in the population, indicating they had a high potential for reproduction (Table 2). A male-biased sex ratio (Table 4) and high keel scores may have provided adult females with the opportunity to behave polygamously and obtain additional matings. Accordingly, adult females were the only birds that attempted to double brood. Though male incubation in the Northern Bobwhite (*Colinus virginianus*) contributes to female abandonment and double brooding (Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995), it is unknown in Gambel's Quail. In the California Quail, a related species that occasionally double broods (Francis 1965), male brood patches are rare and may develop only after the death of a mate (Calkins et al. 1999).

Gambel's Quail at Bosque del Apache exhibited both biparental and uniparental care. Birds also showed communal brooding and the potential for foster care. Communal broods in California Quail can provide fitness benefits (Lott and Mastrup 1999). However, both communal brooding and foster care are unstudied in Gambel's Quail.

In conclusion, the traits related to successful breeding in a wild population of Gambel's Quail were consistent with captive studies that assessed the role of both single and multiple plumage ornaments. Early pairing in males was related to mass and age rather than to ornament size. Male mass was also the primary trait associated with winners of male contests. The mating behavior of Gambel's Quail was flexible. Most birds exhibited a shift in breeding strategy from monogamy to polygamy in three years. Adult females, however, exhibited both strategies with equal frequency. Future investigations should aim to understand the mechanisms that cause shifts in breeding behavior and the costs and benefits of different mating strategies. Studies will require detailed data from radio-tagged breeders under known environmental conditions and estimates of brood paternity, in order to compare the annual and lifetime reproductive success of different sex and age classes.

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