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The kinds of traits involved in male–male competition: a comparison of plumage, behavior, and body size in quail

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I compared the role of ornate plumage, behavior, and body size during male–male competition in two species of New World quail. Gambel's quail (*Callipepla gambelii*) is a highly ornate and dichromatic species, whereas scaled quail (*C. squamata*) is unornamented and monochromatic. During paired contests between unfamiliar males, high rates of testosterone-mediated behaviors (tidbitting, calling) and large body size (mass, tarsus, and tail length) corresponded to winners. In the highly ornate Gambel's quail, male head plumes also influenced the outcome of contests. Plume enhancement made Gambel's quail more likely to win contests, whereas plume removal made males more likely to lose. Plume position also reflected male status. Winning males erected plumes, whereas losers frequently flattened them. Some plumage ornaments, such as belly patches, did not play a primary role during male contests. Unlike static ornaments, head plumes are highly modifiable and likely signal immediate information regarding a male's intent, similar to a coverable badge. Combined, intrasexual selection favored dynamic traits (fast display rates, modifiable ornaments) and static traits (body size) as indicators of male condition or motivation. In scaled quail only, male size was favored both by male–male competition and female choice. Accordingly, the degree of size dimorphism (tarsus length) is greater in scaled than in Gambel's quail. The frequency of overt aggression (chases, pecks, displacement) also differed between species. Gambel's quail were very aggressive, and subordinates often challenged their opponents. In contrast, scaled quail were less aggressive, and subordinates rarely disputed rank. Interspecific comparison indicated differences in the maintenance of male status and possibly in the honesty of signaling. Both appear to be related to differences in social system.
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Intersexual mate choice and intrasexual competition are responsible for the evolution of numerous kinds of secondary sexual traits (reviewed by Andersson, 1994). Some traits appear to be relatively static, such as body size, whereas others are more dynamic or modifiable, such as behavior (Hill et al., 1999). The same is true for ornaments, which may be fixed, as opposed to those that are modifiable with regard to position, size, or hue (e.g., Hansen and Rohwer, 1986; Zucker, 1994).

To understand sexual selection, one must determine the kinds of traits involved and why they are important. Numerous studies suggest that honest or condition-dependent signals often play a role; these include both static and dynamic traits that reliably convey the condition or status of individuals (e.g., Hill, 1991; Ligon et al., 1990). Honest traits may also function in both intra- and intersexual selection (Berglund et al., 1996; Mateos and Carranza, 1999) because reliable assessment of a prospective mate or opponent can result in direct or indirect benefits to the assessor (Hill, 1994; Kirkpatrick and Ryan, 1991; Kodric-Brown and Brown, 1984; Rohwer, 1982).

In birds, the bright or ornate plumage of males often exhibits semipermanent or fixed "badges," such as belly patches, as well as more dynamic "coverable badges," such as the red epaulettes of blackbirds, which are modifiable in size (Hansen and Rohwer, 1986; Rohwer, 1982; Røskaft and Rohwer, 1987). Both kinds of ornaments can signal status (Mateos and Carranza, 1997a,b; Pärt and Qvarnström, 1997; Peek, 1972; Rohwer, 1975) or influence mate choice (e.g., Jones and Hunter, 1999; Mateos and Carranza, 1995; Savalli, 1994). Yet, in some species, ornate plumage traits are not the primary factors involved in sexual selection (Beani and Dessi-Fulgheri, 1995; Buchholz, 1995, 1997; Hagelin and Ligon, 2001; Ligon and Zwartjes, 1995; Ligon et al., 1990; Rohwer and Røskraft, 1989). Like other signals, plumage ornaments appear to vary in their reliability as indicator traits (Badyaev and Hill, 2000; Hansen and Rohwer, 1986; Rohwer, 1982) and may therefore also vary in function as a social signal.

To gain a better understanding of the kinds of traits associated with sexual selection, I examined two species of New World quail that exhibit different secondary sexual characteristics. Gambel's and scaled quail (*Callipepla gambelii* and *C. squamata*) differ drastically with regard to plumage dichromatism, despite their phylogenetic affinity (Zink and Blackwell, 1998). Male Gambel's quail exhibit a long head plume, rusty head patch, and white and dark belly patches, whereas females are dull in color and less ornate. In contrast, both sexes of scaled quail are predominately unornamented and monochromatic (Johnsgard, 1973). Studies of mate choice suggest that male plumage ornaments are not the primary traits involved in female mating decisions of both species (Hagelin and Ligon, 2001). An alternative explanation is that ornaments function during male–male competition.

Male quail are often aggressive before and during the breeding season (Ellis and Stokes, 1966; Johnsgard, 1973). A male-biased sex ratio is also present in wild populations (Brown and Gutiérrez, 1980), providing a basis for intrasexual conflict. The sex bias is more pronounced in the more ornate Gambel's quail (Brown and Gutiérrez, 1980), suggesting that ornaments may be more emphasized during male contests than in scaled quail.

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The primary objective of this study was to explore and compare male–male competition in both quail species in order to understand the kinds of signals involved in intrasexual selection. In a series of two experiments, I examined the role of ornamental, behavioral, and body-size traits involved in contests between two unfamiliar males. First, I identified traits associated with winners and losers of male contests. Next, I manipulated plumage to examine whether ornament alterations affected the outcome of competitive interactions. The two experiments allowed me to characterize traits that correlated with or were causally related to male status.

The study presented here was conducted in parallel with an investigation of female mate choice (Hagelin and Ligon, 2001). A secondary aim was to examine the relationship among sexually dimorphic traits, male status, and female choice. Because intra- and intersexual selection can affect traits either jointly or separately (Moore, 1990), differences in sexual selection can provide insight into patterns of dimorphism between species (e.g., Webster, 1992; but see Badyaev and Martin, 2000). I predicted that if both intra- and intersexual selection favored a particular trait in one species of quail, but not the other, the magnitude of trait dimorphism may differ between the two species.

MATERIALS AND METHODS

Quail were purchased from gamebird breeders as fertile eggs or as 1- to 6-week-olds between June and July 1995–1997. All birds were hatched in incubators and kept in brooders until approximately 7 weeks of age, at which time they were moved to 5 × 7 × 4 m outdoor flight pens. Groups that originated from the same breeder were reared together and visually isolated from other groups. Birds were fed Purina Start and Grow crumble (17% crude protein content), millet, wild vegetation, and water ad libitum. Each individual was banded with a unique combination of colored leg bands as well as a band indicating its rearing group. In January, the sexes were separated into different flight pens. In early March, cohorts of five to seven males that had been reared together were moved to pens identical to those used for male contests (1.25 × 3.25 × 2 m), where they remained for at least 2 weeks before trials began.

Male contests

All male contests took place during the breeding season (late April–late July) of 1995–1998. Pairs of males were randomly selected and consisted of individuals that were unfamiliar with each other. The same pairs of males used in this study were involved in experiments of female mate choice (Hagelin and Ligon, 2001). Males were visually isolated from each other before and during female choice experiments. At least 5 days elapsed before males were used in an intrasexual contest.

I conducted two experiments involving male contests. First, I used pairs of unmanipulated males to identify any relationship among male status and ornament size, body size, or behavior rates. In the second experiment, I manipulated plumage traits to determine any causal relationship between feather ornaments and winners of paired encounters. Males were used only once in each experiment, except in plume removal trials of scaled quail (see manipulation experiments below). Each pair of males was unique, and individuals participated in no more than one contest per day.

Contest protocol

Male contests were conducted on neutral ground in a 1.25 × 3.25 × 2 m arena that was visually isolated from all other birds. The arena contained shelters and perches where individuals could safely withdraw. Birds were observed through a one-way window. After capture and before the start of the trial, each male was isolated for 3 min in a separate 0.5 × 0.5 × 0.5 m cage covered by a towel. Males were then simultaneously released into the arena.

A typical trial lasted 10–15 min. At the start, males usually called and displayed behavioral threats to each other. Displays escalated until birds expressed one of three forms of overt aggression: pecking, chasing, or displacement (described below). A trial ended when an opponent no longer attempted to fight, but rather fled the interaction. This often occurred after the first bout of overt aggression, although some opponents fought back before yielding. Trials were run just long enough to determine an asymmetry in male aggression; no male was injured in any trial.

During male contests, I recorded the following displays for each individual:

- Vocalizations, different calls given by males (Ellis and Stokes, 1966; Schemnitz, 1994). I recorded the number of each call type.
- Simple tidbitting, a ritualized foraging display also used during courtship (Hagelin and Ligon, 2001; Stokes and Williams, 1971). During male contests, simple tidbitting appeared to act as a threat. Aggressors pecked intermittently at the ground when in visual contact with an opponent. After a fight, losing males sometimes pecked at the ground rapidly with a hunched body posture and flattened plume (or crest), as if to indicate submission.
- Formal tidbitting, more ritualized than simple tidbitting, is used during courtship as well (Hagelin and Ligon, 2001). Males fluff out body and flank feathers while pecking at the ground. In Gambel's quail, formal tidbitting is a frontal display accompanied by a unique vocalization, whereas in scaled quail, it is a more quiet, lateral display (Hagelin and Ligon, 2001).

Overt aggression included chases, where an aggressor typically ran after its opponent with its beak open, neck outstretched, and plume (or crest) flattened (Ellis and Stokes, 1966). If an opponent did not fight back, it was often pursued until it sought shelter. Another form was pecking: an aggressor usually pecked its opponent at the back of the head or grabbed at wings or back feathers. Bouts of two or three pecks were common.The third type of aggression was displacement: upon approach of an aggressor, the opponent moved out of the way, apparently to avoid conflict.

Measurements

I measured plumage ornaments and body morphology immediately after a contest. Each individual was measured two more times within 48 h of a trial, and multiple measures of each trait were averaged. For Gambel's quail, ornamental measurements included flattened head plume length (distance from the base of the plume to the tip of the longest plume feather); area of the rusty head patch (mm^2), which is length of the patch (distance from the base of the head plume to the midpoint of the posterior edge of the patch) multiplied by patch width (distance between the tips of the two occipital stripes that outline the sides of the patch); and area of the dark and light belly patch (mm^2). Belly patch areas were determined by multiplying patch length (distance from the midpoint of the leading edge of the patch to the midpoint of the bottom edge) by patch width (distance across the horizontal midline). The dimensions of all patches were measured with digital calipers.

I used two subspecies of scaled quail. Males of *C. s. castanogastris* have a chestnut-colored belly patch, whereas males of *C. s. pallida* do not (Schemnitz, 1994). Measurements for scaled quail included crest length and, where applicable, area

Table 1
Summary of plumage manipulations for male Gambel's and scaled quail

Plumage manipulations	Species	*n*	Protocol
Dark belly patch removal	Gambel's	25	Belly patch covered with ivory colored make-up and translucent powder
Dark belly patch difference	Scaled	21	One male with a belly patch (*C. s. castanogastris*), one without (*C. s. pallida*)
Plume (or crest) removal	Gambel's Scaled	25 20[a]	Plume or crest removed with scissors
Plume elongation	Gambel's	25	Plume feathers trimmed from another male were secured with superglue and black thread, creating a head plume 1.5 times that of normal size (50–65 mm)
Rusty head patch removal	Gambel's	25	Rusty patch covered with grey face paint
Multiple ornament removal	Gambel's	25	Head plume, belly patch and head patch removed, as stated above

n = number of trials.

[a] Each male was used twice during experiment (see Methods, Manipulation experiments).

of dark belly patch. The protocol for each was like that described for Gambel's quail. When I tested for differences in belly patch (see manipulation experiments below), one male of each subspecies was used. For unmanipulated contests, I randomly selected pairs of unfamiliar males.

For both species, body size traits (in mm) included mean tarsus length, mean flattened wing chord, tail length, and culmen length (base of cere to tip of beak). I determined mean measures of tarsus and wing length by averaging the length of left and right appendages. Mass was measured to the nearest gram.

In a preliminary investigation, 10 male pairs of each species were tested 3 times, with at least 2 days elapsing between trials. The winner dominated its opponent in at least two of the three trials. In most cases, the winner of the first trial also won the second trial (17/20 pairs: 7/10 pairs for Gambel's quail, 10/10 pairs for scaled quail), suggesting that the protocol for determining winners was accurate, and dominance status within a pair was fairly stable. Behavior of the two subspecies of scaled quail was indistinguishable, indicating that birds primarily differed with regard to belly patch. To minimize stress to the birds, subsequent experiments involved a single contest between each male pair. All experiments were conducted under Animal Welfare Assurance A4023–01 and University of New Mexico Animal Care Protocol 9801-B.

Manipulation experiments

Pairs of males were matched for body size (tarsus, within 1 mm; weight, within 7 g), and one member of each pair was randomly selected to have one or multiple ornament(s) manipulated. Table 1 describes the plumage manipulations for both species (see also Hagelin and Ligon, 2001). Whenever one ornament was manipulated, care was taken to match males for the size of other ornaments. Head plumes (or crests) were matched within 2 mm. Because the size of dark belly patches was quite variable in both species, I classified males into five categories (1 = smallest patch size, 5 = largest) by matching each individual as closely as possible to photographs of museum specimens that represented each size category. Males in a pair were matched such that their belly patches belonged to the same size category. Due to a limited number of birds at the time of the crest removal experiment, 20 male scaled quail were used twice (Table 1). Each pair of males was unique. During a male's first trial it acted as the control, and in the second trial the male's crest was removed. Only one male lacked a crest in both trials.

Facial ornaments in Gambel's quail

The number of times each male altered its head plume (fully erect versus flattened) or piloerected its rusty head patch (up versus down) was scored in 27 trials of Gambel's quail. Of these, 15 trials involved unmanipulated pairs, and 12 trials involved belly patch manipulations, in which facial ornaments of males remained intact (see manipulation experiments above). I used scores to calculate the rate at which these ornaments were markedly repositioned.

Statistical analyses of male contests

Interspecific comparison of overt aggression

For each unmanipulated male, I summed the number of pecks, chases, and displacements for each individual and divided by trial length to calculate an aggression rate. Because rates were not normally distributed, I used a median test to compare the rates of winning males between species. I also used a median test to compare the relative amount of aggression (winner minus loser male) directed toward competitors. I did not compare interspecific rates of aggression for losers because losing scaled quail retaliated infrequently. Instead, for each species, I tallied the number of losers that exhibited at least one act of aggression toward a winning male. I then tested for interspecific differences via a two-tailed Fisher's Exact test.

Trials of unmanipulated males

For each species, I subtracted the loser's trait from that of the winning male and ran winner minus loser (W-L) scores in two-tailed Wilcoxon signed-rank tests. All behaviors were converted to rates (e.g., number of vocalizations/trial length) and analyzed via the same method. Spearman rank correlations were also run for traits that correlated with winning.

Due to the large number of signed-rank tests, the risk of Type I error is high, and some variables may appear significant by chance (Rice, 1989). However, the Bonferroni adjustment (p = .05/number of tests) may be too conservative, increasing the risk of Type II error. I applied the Bonferroni adjustment to groups of variables that represented different types of male traits (ornamental, body size, and behavioral).

Table 2

Mean trait sizes of unmanipulated male Gambel's quail and the correlation of these traits with winning male contests

Type	Trait	Mean (SD)	*n*	W-L score	*T*	*p*
Ornament	Plume	41.0 (4.0)	39	0.7	100.5	.24
	Dark belly (mm^2)	1271.5 (400.1)	39	51.5	77.5	.36
	White belly (mm^2)	1353.2 (308.0)	38	−21.8	−49.0	.54
	Rusty head (mm^2)	513.0 (57.0)	36	8.5	26.5	.65
Body size	Tarsus	31.7 (1.5)	39	0.5	166.0	.05*
	Mass (g)	161 (11)	35	1.8	35.5	.50
	Tail	82.5 (12.0)	39	−0.5	−2.5	.97
	Wing	113.5 (4.0)	39	0.3	46.0	.57
	Culmen	11.2 (0.9)	39	0.2	112.0	.19
Behavior[a]	Calling	24 (32)	27	13	103.5	.0001**
	Formal tidbit	5 (3)	13	3	36.0	.002**
	Simple tidbit	17 (19)	27	7	107.0	.007**
	Body fluff	5 (3)	39	1	53.0	.06

Ornamental and morphological traits were measured in millimeters, unless otherwise indicated. Winner minus loser (W-L) score indicates how much, on average, winning males differed from losing males. *T* is the value calculated by the Wilcoxon signed-ranks test; *n* = number of trials.

[a] Behaviors calculated as rates (average displays per 15 min).

* Significant at p = .05 level; **significant at the Bonferroni p value for that trait type.

This method provided a biologically meaningful way of decreasing Type I error. I also analyzed W-L scores of all traits simultaneously in a logistic regression with a stepwise selection procedure. Logistic regression identified independent traits that best described winners.

Body size sometimes influences the size of ornaments (e.g., larger birds typically have larger crests). When ornamental and body size traits were both associated with winning, I asked whether winners had larger ornaments than losers, even after accounting for differences in size. I ran a linear regression of ornament size against the first principal component of body size (mass, tarsus, wing). Residuals of this regression represented ornament size after the effect of body size had been removed. Ornament residuals were converted to W-L scores and run in a Wilcoxon signed-rank test to determine if winners still differed from losers. Ornament residuals were also used in multiple logistic regression.

Manipulation experiments

I used binomial tests to determine whether ornament manipulations affected the outcome of trials. When I removed ornaments, I expected males to have an increased likelihood of losing. When I augmented ornaments, I predicted that more ornate males would win. Because each male was used twice during the crest removal experiments of scaled quail, two data sets were analyzed: the first trial of each male (n = 10), and all trials (n = 20).

When a manipulation significantly affected trial outcomes, I examined how the ornament's signal content changed by comparing trial length and behaviors between manipulated and unmanipulated contests. If, for example, manipulations increased the asymmetry between males, contests may be resolved more quickly than unmanipulated trials. Likewise, males may be more likely to challenge opponents that lacked ornaments, but less likely to oppose those with enhanced ornaments. I tested for differences using two-sided t tests of unequal variance. Finally, some Gambel's quail involved in an unmanipulated trial were later used in a plumage manipulation. Therefore, I examined any changes in an individual's status following plume removal or enhancement via a Fisher's Exact test. Changes in status for all other manipulations were examined using a binomial test.

Comparisons of male status and female choice

Because the same pairs of males in this study had been used in a parallel experiment of female choice (Hagelin and Ligon, 2001), I asked whether winners of intrasexual contests were the same as those of intersexual mate choice. For each species, I tallied the number of dominant males that had also been chosen by a female versus those that were not. I evaluated this pattern with a binomial test. I also assessed interspecific differences in intra- and intersexual selection with a Fisher's Exact test.

RESULTS

Interspecific comparisons of overt aggression

Winning males of Gambel's quail exhibited higher rates of overt aggression (pecking, chasing, displacement; mean = 12 acts/15 min) than those of scaled quail (mean = 5 acts/15 min; $Z = 2.75$ $p = .006$). On average, winning Gambel's quail exhibited eight more aggressive acts per 15 min than losers, whereas dominant scaled quail exhibited only three (Z = 3.01, p = .003). Subordinate males also retaliated more frequently in Gambel's quail (14/39 trials = 36%) than in scaled quail (3/40 trials = 8%; Fisher's Exact p = 0.002)

Unmanipulated pairs of males

A total of 79 male–male contests produced clear winners (n = 39 trials of Gambel's quail, n = 40 trials of scaled quail). In both species, rates of male threats, such as calling and tidbitting, were faster in winners than in losers (Tables 2 and 3). All behaviors used in this analysis occurred before either bird exhibited overt aggression, which I used to define the dominance asymmetry. Thus, my protocol avoided the confounding effect of overt aggression altering the subsequent display rates of an opponent.

In Gambel's quail, the size of head plumes and other ornate traits showed no strong relationship with winning (Table 2). However, winning males erected their head plumes and rusty head patches more frequently than losers (plume: t = 18.0, p = .008; rust: t = 30.5, p = .03). Likewise, losers flattened plumes and head patches more often than winners (plume: t

Table 3

Mean trait sizes of unmanipulated male scaled quail and the correlation of these traits with winning male contests

Type	Trait	Mean (SD)	*n*	W-L score	*T*	*p*
Ornament	Crest	27.5 (2.0)	40	1.8	278.0	.0001**
	Dark belly (mm^2)[a]	1173.3 (332.6)	40	258.6	57.0	.32
Body size	Tarsus	33.0 (1.4)	40	0.6	144.5	.05*
	Mass (g)	184 (18)	40	7.8	143.0	.05*
	Tail	86.0 (20.5)	40	2.0	156.0	.02*
	Wing	117.0 (4.0)	40	1.7	136.5	.06
	Culmen	13.0 (0.8)	40	0.3	124.5	.10
Behavior[b]	Calling	12 (15)	31	16.0	135.5	.0001**
	Formal tidbit	4 (4)	12	5.0	33.0	.001**
	Simple tidbit	4 (4)	40	2.0	95.5	.07
	Body fluff	3 (2)	35	2.0	153.0	.01**

Ornamental and morphological traits were measured in millimeters, unless otherwise indicated. Winner minus loser (W-L) score indicates how much, on average, winning males differed from losing males. *T* is the value calculated by the Wilcoxon signed-ranks test; n = number of trials.

[a] Dark belly patch measurements for *C. s. castanogastris* only.

[b] Behaviors calculated as rates (average displays per 15 min).

* Significant at $p = .05$ level; **significant at the Bonferroni p value for that trait type.

$= -27.5$, $p = .002$; head patch: $t = -50.0$, $p = .008$). Tarsus length, a measure of body size, was also slightly larger for winners of Gambel's quail contests (Table 2).

Crest length of scaled quail was the only ornament of either species that correlated with winning (Tables 2 and 3). Winning scaled quail were also larger in size than losers (Table 3). Because body-size traits correlated with crest length ($n = 60$, $r_S \geq .32$, $p \leq .01$), I ran a principal component analysis of body size (mass, tarsus, wing), followed by a linear regression of crest length on the first principal component of body size (PCA1). PCA1 represented male size, as it was positively weighted for each trait (.7 tarsus, .6 mass, .3 wing). It also described 54% of the variation in mass and tarsus and wing length. The regression of crest length versus PCA1 was significant ($r^2 = .15$, $F_{1,118} = 21.3$, $p < .0001$). W-L scores of crest residuals suggested that, even after accounting for body size, winning scaled quail had slightly longer crests (1.1 mm on average), than losers ($n = 59$, $T = 428$, $p = .0008$).

Logistic regression of multiple traits

For Gambel's quail, 22 trials of unmanipulated males contained a complete set of ornamental, body size, and behavioral rates (simple tidbitting, body fluffing, calling). The stepwise selection procedure produced a significant model describing winning males ($-2\log L$ $\chi^2_2 = 28$, $p = .001$). Call rate (Wald $\chi^2_1 = 8.95$, $p = .002$) and tarsus length (Wald $\chi^2_1 = 5.49$, $p = .02$) were the best predictors of male status. Formal tidbitting was not included in the logistic model because it was recorded in only 13 trials (Table 2). However, in 12 of these, formal tidbitting was exhibited only by the winning male (sign test, $p = .004$, see also Table 2). Formal tidbitting also tended to correlate negatively with trial length ($r_S = -.53$, $p = .07$) and positively with simple tidbitting ($r_S = .5$, $p = .08$), but it was unrelated to male size ($p > .4$). Rate of overt aggression also did not correlate with male size ($p > .5$).

For scaled quail, 23 trials of unmanipulated males were used in the logistic regression. Crest residuals (rather than crest length) were used because of the relationship between crest size and body size (see above). The logistic procedure selected a significant model that described the traits of winning males ($-2\log L$ $\chi^2_2 = 18.58$, $p = .0001$). Call rate (Wald $\chi^2_1 = 7.02$, $p = .008$) and mass (Wald $\chi^2_1 = 3.76$, $p = .05$) were the best predictors of male status. Formal tidbitting was not included in the model, as it occurred only in 12 trials. In 11 of these, formal tidbitting was exhibited only by the winning male (sign test, $p = .006$, see also Table 3). The rate of formal tidbitting correlated negatively with trial length ($r_S = -.72$, $p = 0.01$), and although it was unrelated to simple tidbitting ($p = .2$), it correlated positively with male size (tarsus: $r_S = .54$, $p = .05$; mass: $r_S = .64$, $p = .04$) and rate of overt aggression ($r_S = .59$, $p = .04$). Overt aggression also exhibited a negative relationship with size ($n = 50$; tarsus: $r_S = -.29$, $p = .04$; mass: $r_S = -.27$, $p = .06$).

Manipulation experiments

Although 20–25 trials were run for each manipulation (Table 1), only those that produced clear winners were analyzed (Table 4). In Gambel's quail, males without plumes were more likely to lose contests, whereas those with elongated plumes were more likely to win (Table 4). Crest removal in scaled quail as well as other plumage manipulations in both species did not appear to alter the outcome of male contests (Table 4).

For plume manipulations of Gambel's quail, contests were shorter in length (elongation: 6.85 min; df = 45, $t = 2.0$, $p = .05$; removal: 5.79 min; df = 44, $t = 2.77$, $p = .008$) than contests of unmanipulated males (9.42 min). Male behaviors also differed from unmanipulated contests. Losers whose opponents had elongated plumes showed lower rates of overt aggression than losers of unmanipulated contests (0 versus 1 aggressive act/15 min, df = 27, $t = 1.7$, $p = .002$). These losers also tended to call less often (1 versus 6 calls/15 min; df = 37, $t = 1.82$, $p = .08$). Winning males with elongated plumes did not differ in behavior, however, from unmanipulated winners ($p > .3$). During plume removal, losers (that lacked plumes) exhibited less aggression than losers of unmanipulated trials (0 versus 1 aggressive act/15 min, df = 36, $t = 2.89$, $p = .006$). This may have occurred because their plumed opponents tended to exhibit higher rates of simple tidbitting than winners of unmanipulated trials (50 versus 21 tidbits/15 min; df = 17, $t = 1.78$, $p = .09$). Call rates and overt aggression of winners did not differ between manipulated and unmanipulated trails ($p > .2$).

Gambel's quail used in both types of trials were affected by plume alterations. Males without head plumes were more like-

Table 4

The number of manipulated versus control males that won male contests

Experiment type	Male contest winners		Z	p
	Manipulated	Control		
Gambel's quail				
Plume removal	8	17	1.80	.04
Plume extension	15	9	1.63	.05
Multiple ornament removal[a]	10	13	0.63	.26
Belly patch removal	9	13	0.85	.20
Rusty head patch removal	12	12	0.0	.50
Scaled quail				
Belly patch difference[b]	12	10	0.58	.66
Crest removal[c]	10 (5)	10 (5)	0.0	.50

See Table 1 and Methods for a description of manipulations; *p* values are one-tailed estimates of the binomial distribution.

[a] Plume, dark belly patch, and rusty head patch removed.

[b] One male of each subspecies used in contest (see Table 1 and Methods).

[c] Males were used twice during crest removal; the outcome for the first trials of males are given in parentheses.

ly to become subordinate and/or maintain their subordinate status (14:6), whereas males with elongated plumes exhibited the opposite pattern (7:12; one-tailed Fisher's Exact $p = .04$). For all other manipulations, male status was more likely to remain the same between trials, rather than change (21:9, $Z = 2.19$, $p = .02$).

Correlation between female choice and male dominance

Of the 39 pairs of unmanipulated Gambel's quail, 18 winning males (46%) were also chosen by females. Of the 40 pairs of scaled quail, 28 winning males (70%) were chosen by females. The number of winning males associated with female choice differed between the species (Fisher's Exact $p = .03$). In Gambel's quail, female choice and dominance showed no relationship ($p = .73$). However, in scaled quail, female choice and dominance were correlated more often than expected by chance ($Z = 2.52$, $p = .01$).

Differences in the pattern of male dominance and female choice may reflect differences in size dimorphism between the two quail species. In scaled quail, larger males were favored by both male–male competition (Table 3) and female choice (Hagelin and Ligon, 2001), whereas in Gambel's quail, body size was favored only in male–male competition (Table 2; Hagelin and Ligon, 2001). Therefore, I expected the magnitude of size dimorphism to be greater in scaled quail than in Gambel's quail. A comparison of tarsus length in both captive-reared birds and museum specimens suggests that scaled quail do, indeed, exhibit greater size dimorphism than Gambel's quail (Table 5).

DISCUSSION

Close examination of male–male competition revealed both striking similarities and differences between Gambel's and scaled quail. Although Gambel's quail was nearly twice as aggressive as scaled quail, high rates of displays and large body size were related to winning in both species (Tables 2 and 3). With regard to ornaments, the head plume of Gambel's quail was a primary plumage trait that affected the likelihood of winning (Table 4). Finally, both intra- and intersexual selection appear to operate differently in the two species, with females preferring large, dominant males in scaled quail, but not in Gambel's quail. Although the above information is complex, it reveals insight into the kinds of traits that sexual selection favors, as well as the patterns that underlie male and female behavior.

Traits used in male contests

The traits involved in intrasexual selection are thought to signal information, such that opponents settle contests and avoid unnecessary or costly interactions (Andersson, 1994; Berglund et al., 1996; Maynard Smith, 1982). Such traits may be reliable or honest if they impose costs to the signaler. For example, behavior can result in direct physiological costs (Buchanan, 2000; Folstad and Karter, 1992; Peters, 2000; Vehrencamp et al., 1989; Wingfield et al., 1997). Traits may also involve indirect social costs (e.g., Leonard and Horn, 1995), in which the signaler bears the burden of underwriting its interests (Deag and Scott, 1999) and honesty is maintained via social remediation (Waas, 1991; Zahavi, 1977). Alternatively, when costs are low, dishonest signaling may occur if cheating is profitable (e.g., Candolin, 2000).

Behavior

In both Gambel's and scaled quail, high rates of calling and tidbitting were closely associated with winning (Tables 2 and 3). The rate of formal tidbitting also showed a negative relationship with trial length, indicating that opponents with large display asymmetries settled contests quickly. Although the energetic costs of fast display rates are unknown, studies of castrated Gambel's and scaled quail suggest that displays are related to testosterone (Hagelin, 2001). Although unstudied in

Table 5

Mean tarsus length and percent sexual dimorphism of captive and museum specimens of Gambel's and scaled quail

Type	Gambel's quail			Scaled quail			Z	p
	Male (n)	Female (n)	Dimorphism[a]	Male (n)	Female (n)	Dimorphism[a]		
Captive	31.8 (93)	31.0 (62)	3.2	33.1 (91)	31.5 (57)	5.0	1.7	.05
Museum	32.4 (63)	32.0 (53)	1.2	33.8 (53)	32.6 (27)	3.5	2.3	.01[b]

Mean tarsus length is given in mm; *p* values are one-tailed and indicate differences in the amount of sexual dimorphism between the two species. Captive birds were first-year birds only; museum specimens were a mix of adult and first-year birds.

[a] Percent sexual dimorphism: $(1 - \text{male/female})100$.

[b] Statistical significance was greater for museum samples, because the variance of adult measurements was low, making estimates of dimorphism more precise.

New World quail, testosterone can impose costs on immune function (Verhulust et al., 1999). Furthermore, testosterone has been linked to honest traits that maintain male status in several other galliform species (Alatalo et al., 1996; Buchholz, 1997; Ligon et al., 1990).

In both quail species, high display rates were successful during both male–male competition (Tables 2 and 3) and female choice (Hagelin and Ligon, 2001). This pattern provides further support that male behaviors may contain functional, rather than arbitrary information (Berglund et al., 1996; Hill, 1994; Kodric-Brown and Brown, 1984; Mateos and Carranza, 1999). To more accurately assess signal honesty, future tests need to examine whether deceitful displays impose social costs and whether females benefit from mating with males with high display rates (Berglund et al., 1996; Hagelin and Ligon, 2001).

Body size

Size is often attributed to intrasexual selection because bigger males have an increased likelihood of overpowering smaller competitors (Andersson, 1994; Ligon, 1999). Likewise, size is frequently considered honest because it is connected to an underlying quality of an individual that can be difficult to fake (Maynard Smith and Harper, 1988; Taylor et al., 2000). In both species of quail, male size was associated with status (Tables 2 and 3). Size also correlated negatively with the rate of overt aggression in scaled quail, suggesting that larger males did not have to assert aggression as often as smaller males did to win.

When a pair of male quail face off, or spar, they often stand on tiptoe and stretch their necks high into the air, making their bodies appear as tall as possible (Delehanty, 1997; Gutiérrez and Delehanty, 1999). Such behaviors have the potential to honestly reveal size in the process (Guilford and Dawkins, 1995; Taylor et al., 2000). However, dishonest signaling may also be possible because individuals can presumably adjust their appearance during an interaction.

Ornaments

Although a variety of explanations have been proposed for the evolution and maintenance of plumage traits involved in male contests (e.g., Butcher and Rohwer, 1989; Huxley, 1938; Johnstone and Norris, 1993; Peek, 1972; Maynard Smith, 1982), all suggest that ornate feathers signal intent or status. In this study, the head plume of Gambel's quail was a primary plumage trait involved in male contests. Winners erected their plumes more frequently than losers. Experimentally elongated plumes were also associated with winning, whereas plume removal increased the likelihood of losing (Table 4).

Head plumes are extremely modifiable and dynamic. They are similar to a coverable badge (Hansen and Rohwer, 1986; Rohwer, 1982) in that they can change rapidly to serve as "notice" to an opponent (Maynard Smith, 1991), rather than simply act as a static badge of status. Dynamic traits on the face or head are key signals involved in intrasexual contests of several galliform species (Buchholz, 1997; Ligon et al., 1990; Mateos and Carranza, 1997b). Such ornaments may be favored if they provide more accurate or immediate information regarding male motivation than a static badge.

Manipulation experiments suggest that Gambel's plumes are used to assess intent. Apparently wary of an augmented signal, winners threatened males with enhanced plumes less often than in unmanipulated trials. However, when an opponent lacked a plume, winners tended to exhibit more displays, as if they were more certain of winning. It is unclear, however, whether plumes act as honest signals. In other investigations, exaggerated ornaments caused males to suffer social costs because they were frequently tested and/or experienced escalated fights with males of higher status (e.g., Møller, 1987; Rohwer and Rohwer, 1978; Watson and Parr, 1981). Had contests run longer, perhaps opponents would have exposed the dishonesty of augmented plumes.

Clearly, the plumes of quail vary not only in orientation (up versus down) but also in size. For Gambel's quail, however, natural variation in plume size may not be as informative as altering plume position. Consistent with this prediction, I found no evidence that plume length correlated with winning in trials of unmanipulated males (Table 2). Likewise, in a 3-year field study, plume length was not related to male status or mating success (Hagelin, 1999). Instead, plume manipulations may have created a supernormal signal with regard to position. Elongated plumes of Gambel's quail hung far forward, similar to an erect-crested, dominant individual. In contrast, plume removal may have created an extreme signal of submission (a completely flattened or deemphasized plume).

The role of crests in scaled quail is more difficult to interpret. Winning males had slightly longer crests (1.8 mm; Table 3). However, manipulation experiments suggested that contest outcome was not dictated by crest length; males with crests won as frequently as those without (Table 4). Consequently, crest size correlated with, but did not appear to be causally related to, male status. The positive relationship between crest size and status (Table 3) may be due to greater feather wear of subordinates (Hagelin and Ligon, 2001). Abrasion can alter the size of ornate feathers, potentially making them less reliable indicators (Buchholz, 1997). Future studies require data on crest displays, as well as a larger sample of crest manipulations. Because crests of scaled quail are similar to the dynamic plumes of Gambel's quail, they may also play a role in intrasexual signaling.

Ornaments not clearly involved in sexual selection

In both species of quail, males exhibit dimorphic plumage traits, such as belly patches, that did not appear to be involved in either male–male competition (Tables 2–4) or female choice (Hagelin, 1999; Hagelin and Ligon, 2001). This curious result demands explanation. I ran a power analysis to determine the degree to which male ornaments could vary in experiments, while remaining 80% certain that I did not falsely accept the null hypothesis of no difference between winners and losers. Correlational data (Tables 2 and 3) were capable of detecting medium-size ornamental effects (Cohen, 1988). That is, differences were detectable, even though ornament sizes of winners and losers overlapped 62–66%. Manipulation trials (Table 4) could detect relatively large effects between manipulated males and controls, or a 3:1 departure from the null of 1:1 (Cohen, 1988). Larger data sets are required to assess smaller effect sizes, including why multiple ornament manipulations of Gambel's quail, which included plume removal, did not produce a stronger result (Table 4). However, it appears that some feather ornaments do not play as prominent a role during male contests as behavior rate, body size, or head plumes.

The lack of a relationship between the dimorphic plumage of males and sexual selection has been noted in several avian species (Beani and Dessi-Fulgheri, 1995; Buchholz, 1995, 1997; Ligon et al., 1990; Ligon and Zwartjes, 1995; Rohwer and Røskraft, 1989). Such results suggest that the conventional mechanisms of sexual selection (mate choice, male contests) may not entirely account for the maintenance of dimorphic plumage. Other mechanisms may be involved. For example, bright males may be favored, if they are less profitable prey, compared to dull-colored females at nests (Baker and Parker, 1979). Male plumage may also function in other social interactions, such as cryptic female choice (Eberhard, 1996), may operate in long-distance communication (Dale and Slagsvold, 1996), or may reflect status during the nonbreeding season (e.g., Senar and Camerino, 1998). If, however, ornaments reliably indicated status during nonbreeding, it is unclear why they would not also function during sexual selection (Hagelin and Ligon, 2001). Honest signals frequently play a role in multiple social contexts because assessors benefit by receiving reliable information about the quality of competitors or mates (Berglund et al., 1996; Pärt and Qvarnström, 1997; Mateos and Carranza, 1999).

If an ornament spreads among individuals in a population, it may lose both honesty and function, causing males to switch to other signals, similar to an evolutionary arms race (Butcher and Rohwer, 1989; Grether, 1996; Rohwer and Røskaft, 1989; Johnstone and Norris, 1993). Yet, functionless ornaments may persist if they are cheap to produce and subject to weak selection (Brooks and Caithness, 1995; Møller and Pomiankowski, 1993). If some ornaments of quail have lost their function, it is unclear how weak selection must be in order to maintain them.

Interspecific patterns of behavior and size

Male–male competition and female choice correlated with male status in scaled quail, but not in Gambel's quail. Consequently, both intra- and intersexual selection favored larger males in scaled quail (Table 3; Hagelin and Ligon, 2001). However, in Gambel's quail, only male–male competition favored larger males (Table 2). Based on the above pattern, I expected the magnitude of selection on male size to be stronger in scaled quail than in Gambel's quail. Consistent with prediction, the degree of size dimorphism was greater in both captive and wild populations of scaled quail (Table 5).

It is puzzling why two closely related species should diverge so dramatically with regard to patterns of sexual selection. Why, for example, do female scaled quail prefer dominant males, but Gambel's females do not? The result may be related to differences in signal honesty, the maintenance of male status, and mating system. In scaled quail only, winners of both intra- and intersexual selection were associated with large size, a common indicator of quality (see above). Furthermore, formal tidbitting, a key behavior related to winning, also correlated with male size (mass, tarsus) in scaled quail, but not in Gambel's quail. The relationship between size and behavior may facilitate honest signaling in scaled quail, particularly if large males enforce the status that they signal. Losing scaled quail only rarely challenged winners, as if they accurately assessed their opponents' status. I also observed strict social relationships in scaled quail during nonbreeding, when captive birds exhibited a linear hierarchy that was more rigid than in Gambel's quail (Hagelin, unpublished data). In the field, honest signaling of status may also be emphasized in the social relationships of scaled quail. Both sexes appear to be inseparable from a single mate (Evans, 1997). In systems with high levels of social (and presumably genetic) monogamy, both accurate signaling and assessment of status are likely to be advantageous to both sexes (Jones and Hunter, 1999).

Unlike scaled quail, size and display rate were not correlated in Gambel's quail, indicating that assessment of opponents or mates may be more difficult. Winning males exhibited high rates of aggression, as if to quell the frequent retaliation of losers. Compared to scaled quail, persistent attacks may be beneficial in Gambel's quail, given that the sex ratio of wild populations is more male biased (Brown and Gutiérrez, 1980). Escalated fighting would appear to have a greater payoff. Though costly, aggression can increase the chances of a lower ranking male obtaining higher status (Senar et al., 1992).

If, however, the result of male–male competition does not reliably reflect male quality, females may not prefer dominant males (Qvarnström and Fosgren, 1998). High rates of aggression might lower mate quality in Gambel's quail, if, for example, dominant males experience trade-offs between aggression and parental effort (Qvarnström and Fosgren, 1998). Finally, compared to scaled quail, Gambel's quail may have a more flexible, polygamous mating system, in which both males and females form sequential mating associations during a single breeding season (Hagelin, 1999). Taken together, both captive and field data suggest that social relationships of Gambel's quail may be more contestable and transitory than in scaled quail. The key environmental mechanisms that underlie these divergent behaviors, however, are unstudied.

In conclusion, primary traits favored by intrasexual selection in both Gambel's and scaled quail, such as behavior rate and body size, have the potential to act as honest signals if the traits impose physiological costs and/or there is social control of deception. The same is true for the head plume of Gambel's quail, the primary ornament associated with male status. The head plume is a dynamic trait, capable of providing immediate information about male intent. Some plumage ornaments, such as plumes, may play a more prominent role in sexual selection than others, particularly if they function as reliable, dynamic indicators. In both quail species, interspecific differences in sexual selection were consistent with patterns of body-size dimorphism. However, striking behavioral patterns, such as the correlation between female choice and male–male competition in scaled quail only, require further study. Differences in behavior, such as the rates of overt aggression, may be related to the stability of social relationships in each species and presumably result from different ecological pressures.

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