THE STRUT DISPLAY OF MALE SAGE GROUSE: A "FIXED" ACTION PATTERN

by

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(With 6 Figures)

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The behavioral repertoire of the Sage Grouse (*Centrocercus urophasianus*, Tetraonidae) includes one of the most complex stereotyped motor patterns found among birds. Although this display, the Strut, has now been described by a number of authors (see references below), none has attempted any measurements of its variability. Such an analysis reveals the extraordinary precision of this coordination, both within the repeated performances of one individual and in different individuals and populations, and suggests a proprioceptive mechanism that might help to explain the development and control of this extreme stereotypy. In addition, the Strut display can exemplify the selective forces behind the evolution of many "fixed" action patterns.

During the breeding season male Sage Grouse occupy small territories each morning and evening on a communal display ground, or lek (SCOTT, 1942; PATTERSON, 1952; LUMSDEN, 1968; HJORTH, 1970; WILEY, in press). Females visit these leks to copulate and then tend their nests and broods without help from any male. Only a few males on each lek copulate with most of the females, while most males never copulate during any one season. First-year males, recognized in the field by their incompletely developed plumage (PATTERSON, 1952; DALKE *et al.*, 1963; ENG, 1963; WILEY, in press), apparently never copulate. The above references discuss in more detail the social interactions on Sage Grouse leks.

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PROCEDURES

Measurements and descriptions of behavior patterns were based on 7900 feet on 16-mm film exposed during the springs of 1967-1969 near Laramie and Farson, Wyoming, and Grass Range, Montana. For detailed analyses of motor patterns, film shot at 24 frames/second or 32 frames/second proved essential. For information on the association of behavior patterns with different contexts, I examined some 35 hours of time-lapse film (one frame every 1-5 seconds).

Acoustic signals were recorded on a Nagra III tape recorder at 7½ i.p.s. and analyzed on a Kay Electric Company sound spectrograph with the broad-band filter (effective resolution: 300 Hz). In order to measure intervals between Struts and beween distinctive acoustic signals within a Strut, I analyzed tape-recorded sequences of two Strutting males by displaying the amplified output from a tape recorder on a Sanborn 151 galvanometric recorder. As the latter had a frequency response of about 100 Hz, the resultant tracing represented a crude amplitude envelope of the tape-recorded signal.

Individual males were recognized by distinctive patterns formed by the white spots on their under tail-coverts (Wiley, in press). These patterns, clearly visible in the Strutting Posture (see below), remained stable throughout any one season, in spite of temporary disturbances caused by the wind and by postures in which the tail was folded.

Lumsden (1968) and Hjorth (1970) have both coined terms for Sage Grouse behavior patterns. The terms used in this paper, which coincide only partly with these authors', were chosen for simplicity and to avoid as much as possible implications about the motivations or evolutionary origins of the behavior.

COORDINATION OF THE STRUT DISPLAY

Both Lumsden (1968) and Hjorth (1970) have presented detailed descriptions and illustrations of this display (Lumsden: Strutting Display; Hjorth: Ventro-forward). The present discussion will attempt a more functional description than either of these authors' accounts. My conclusions accord almost completely with those of Clarke *et al.* (1942), who deduced from anatomical studies many of the mechanisms involved.

The display begins from the Strutting Posture (tail fanned and cocked vertically, head raised, neck plumage erect; Figure 1) and consists in coordinated movements of the wings and the large esophageal sac, together with associated movements of the legs, head and trunk (Figures 2 and 3). The esophageal sac is inflated in the course of being twice lifted and dropped. Concurrently, the wings are extended forward and retracted twice. The culmination of the display follows immediately: a rapid compression and ballooning of the sac accompanied by a third excursion of the wings. Complex acoustic signals accompany this culminating action. These include two sharp snaps produced by the inflated air sac and an intervening whistle that rises and falls in pitch. This final 0.2-second part sounds roughly like *poink*. Preceding this sound are three low-pitched coos, probably produced by the syrinx, and two swishing sounds generated by the wings rubbing against the sides of the chest (Figure 4).

Figure 1. The Strutting Posture.

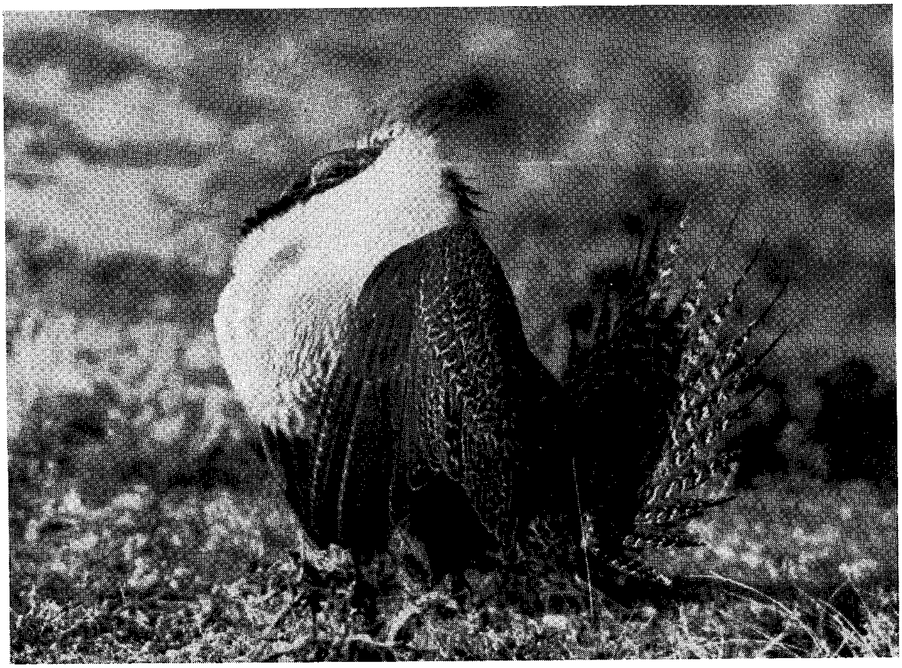

Figure 2. The Strut, Stage IIA (see Table 1 and Figure 5).

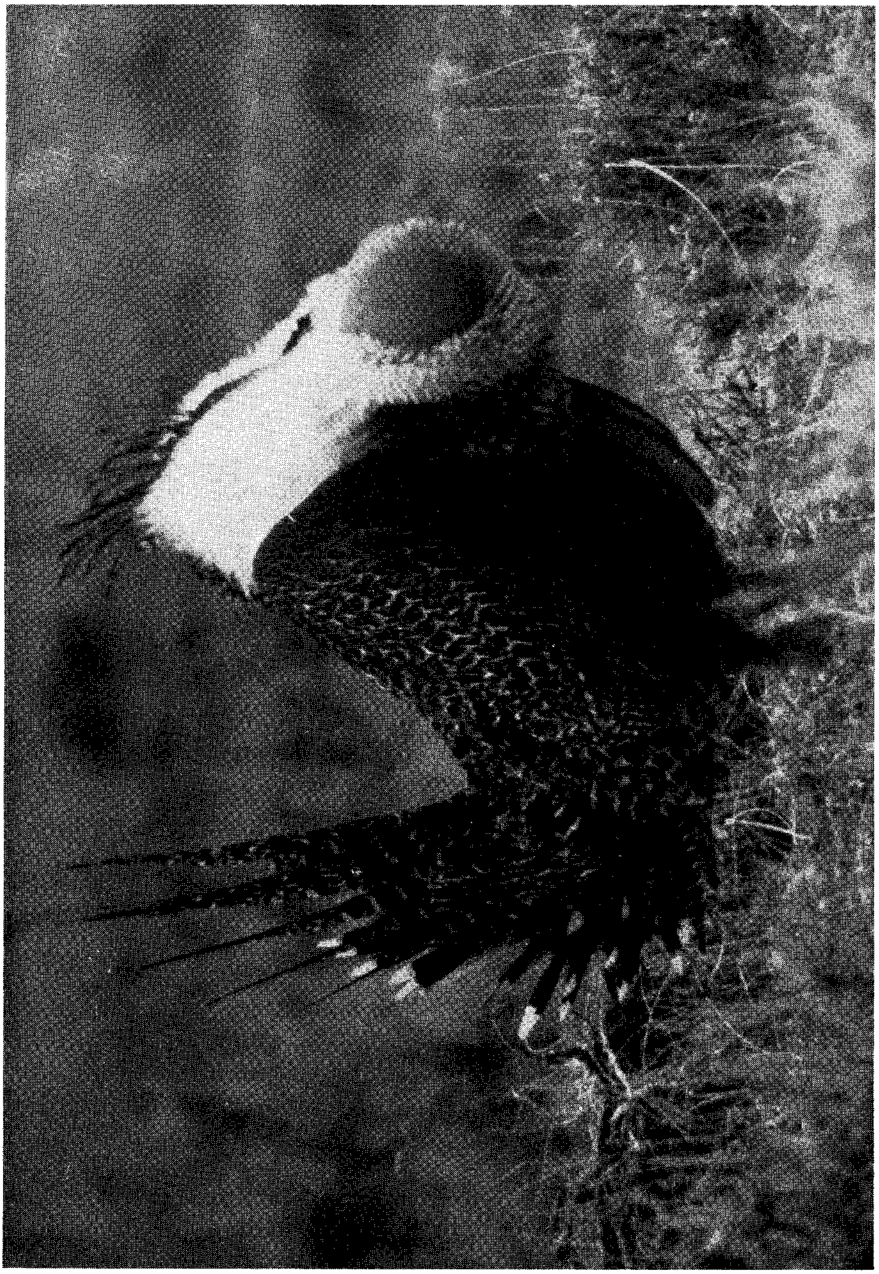

Figure 3. The Strut, Stage IIIB (see Table 1 and Figure 5).

The components of the display are summarized in Table 1 and graphically in Figure 5, which presents the vertical excursions of the chest sac, the changing width of the bare areas (an index of the expansion of the sac), and the acoustic accompaniment. Preceding and partially overlapping the first excursion of the chest sac, the male takes a variable number of steps forward and usually turns to one side or the other. The entire coordination lasts over 3 seconds.

TABLE 1

Outline of the Strut display of male Sage grouse

I. First Cycle of Inflation
  A. Preliminary steps
  B. Sac lifted first time
  C. Sac drops
  D. Sac recoils upward and drops again

II. Second Cycle of Inflation
  A. Sac lifted second time (Figure 2)
  B. Sac drops

III. Culmination
  A. Sac compressed
  B. Sac balloons outward into bare areas (Figure 3)
  C. Damped reverberations of expansion and collapse

IV. Relaxation to Strutting Posture

The various movements seem aimed at inflating and finally compressing the large sac. An analysis of these processes requires some introduction to the anatomy of the chest region. The enormous esophageal sac reaches 4 to

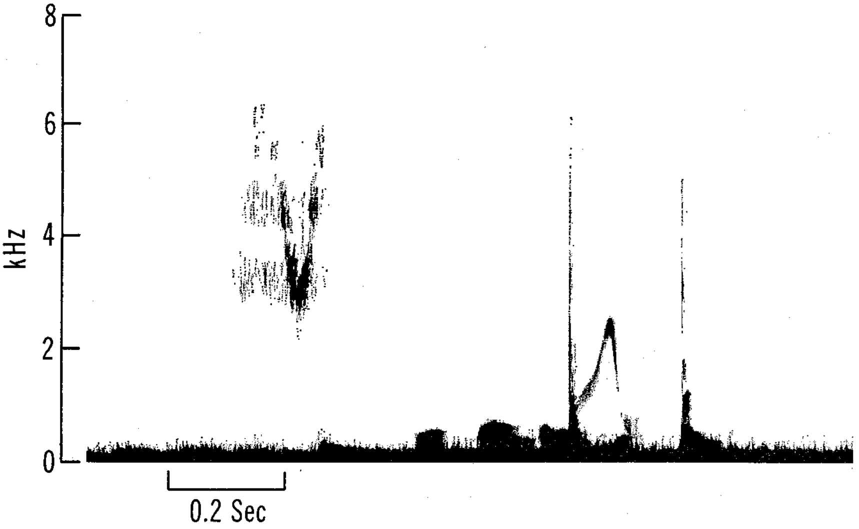

Figure 4. Spectrogram of acoustic production during the Strut. The first wing scrape is not included.

5½ liters in size in a breeding male (Clarke *et al.*, 1942). Two bare oval patches of olive-colored skin overlie the sac. The superficial muscles of the neck region, on the basis of descriptions by Honess & Allred (1942), fall into three categories according to their locations with respect to the bare areas. The fibers of one group pass medially between the two bare areas. Included here is a muscle well developed in males, although nearly absent in females, that arises from the sternum and inserts along the entire length of the trachea where it crosses the ventral surface of the large esophageal sac. Another group of muscles passes lateral to the bare areas, and a third group is oriented primarily transversely across the lower chest below the bare membranes. No muscles actually cross the bare areas themselves. Simultaneous contraction of these three groups of muscles would compress the esophageal sac against the vertebral column. Heavy circular musculature caudal to the sac traps air in the sac during inflation. The sac itself and the overlying connective tissue contain abundant elastic fibers.

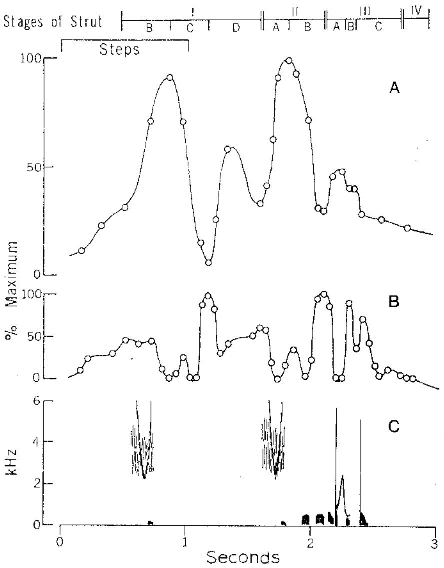

Figure 5. Correlation of sac movements and acoustic production during the Strut. A, height of sac above the ground, expressed as percentage of the maximum. B, width of each bare area (an index of the expansion of the sac), expressed as percentage of the maximum. C, acoustic production (see Figure 4). At the top the stages of the Strut (see Table 1) are indicated. The measurements in A and B are taken from a film sequence of a typical Strut.

Inflation of the esophageal sac appears to occur in two steps. Air is first inhaled into the lungs and air sac system as the chest sac is lifted and compressed by the superficial musculature (Figure 2). During this phase the neck is extended upward and the body axis tilts upward in front, both movements that seem to aid in taking a deep breath. Coinciding with the peak of the sac's excursion, the beak rotates upward and opens momentarily. In the second phase, the chest sac drops, the superficial muscles relax, and the neck and body are lowered. These actions seem to press air from the lungs into the esophageal sac through the glottis and pharynx. Special pads on either side of the glottis occlude the pharynx anteriorly and provide a channel from the glottis into the esophagus (CLARKE *et al.*, 1942). For additional inflation, these two phases are then repeated as the chest sac is lifted and dropped a second time.

CLARKE *et al.* (1942), who discovered the pharyngeal pads and deduced the transfer of air from the lungs to the esophageal sac, believed this transfer to occur as the sac was lifted, rather than as it was dropped. However, the superficial muscles clearly contract during the lifting of the chest sac, so that, if the esophagus were allowed to open anteriorly at that time, air would escape from the sac rather than enter it. Instead, as I have surmized above, the pressure gradient from the lungs to the esophagus would probably inflate the sac as it drops.

During these two cycles of inflation, the only sounds come from the carpi scraping across the sides of the chest to produce a sharp swish accompanied by a resonant thump (about 100-150 Hz; Figure 4) each time the sac is lifted. Between the two cycles the chest sac recoils upward slightly, apparently as a result of its own elasticity and inertia, then falls again.

At the end of the second cycle of inflation, as the chest sac drops for the second time, three cooing sounds issue from the syrinx. The second coo is the loudest acoustic component of the display other than the two snaps. In adult males it lasts about 0.05 seconds at a frequency of about 450 Hz (Figure 4). The first (0.045 seconds, about 300 Hz) and third (0.03 seconds, falling from 300 Hz initially) coos are much softer than the second. Immediately following the third coo, a violent jerk of the chest sac produces a loud *poink*, the culmination of the display. This sound consists of two sharp snaps about 0.19 seconds apart with a rising and falling whistle in the first half of this interval (Figure 4). The whistle starts between 750-1050 Hz, rises to between 2050-2350 Hz, and finally drops to between 450-600 Hz. At the termination of the whistle a brief, low-pitched (about 200 Hz) note is produced. The second snap seems to have more energy at lower frequencies than the first snap, a difference that becomes evident when listening to a tape-recording at slow speed.

The mechanism that produces the strange resonant *poink* has had no fully satisfactory explanation. The following suggestions are based on detailed comparisons of sound spectrograms and slow-motion films of the sac movements. Immediately after the displaying male has completed his second cycle of inflation, the superficial muscles of the chest tighten over the sac and compress it against the spinal column. The bare areas completely disappear from view. The compressed air is then released suddenly against the relatively thin, elastic bare areas (Figure 3). The moment of this release apparently coincides with the first snap, which just precedes the sudden expansion of the bare membranes, while the rising and falling whistle coincides with this first expansion (Figure 5). The displaying male puts a major effort into this culminating maneuver. The wings extend forward during the compression of the air sac and then retract vigorously just before the bare membranes balloon outward from the tense chest. The neck extends forward as the chest sac is compressed against it. When the sacs balloon outward the head rotates downward abruptly, a movement that would probably prevent air from escaping through the mouth. Immediately, there ensues a damped reverberation in the expansion of the sac with a period of approximately 0.2 seconds. The final snap just precedes the second expansion, and quickly thereafter the reverberations damp out. Both snaps therefore seem associated with the sudden release of air under pressure.

VARIATION IN THE STRUT DISPLAY

A striking feature of Strutting is its rhythmicity, both in the coordination of the display itself and in its serial repetition. To the observer in the field the coordination of the Strut, both in repeated performances by the same male and in performances by different males, seems extraordinarily stereotyped, while the timing of successive displays seems more variable. I have attempted to measure the variation, both in individual males and among different males, in the gross movements, acoustic production, and timing of successive Struts. These measurements bear out the impression that some features of Strutting show much greater variability than others. Within my limited samples, I can detect no tendency for slight individual differences in the Strut display to have systematic associations with mating success, beyond the clear evidence that the performances of first-year males differ in several respects from those of older males.

Struts by males at least two years old.

Stereotypy in the temporal coordination of this display was estimated most accurately by examining galvanometric tracings from tape-recordings of single males (see Procedures). A discrete peak in the galvanometric tracing corresponded to each acoustic component of the Strut. I measured, in units of 0.02 seconds, the interval from the peak of the first swish produced by the wings to the peak of the first snap, an interval of about 1½ seconds.

In 45 consecutive Struts by adult male C (Ford's Creek Lek, 15 April 1968), the mean interval was 77.3 units (1.55 seconds) with a standard deviation of 0.55 units (coefficient of variation, 0.7 of one percent).

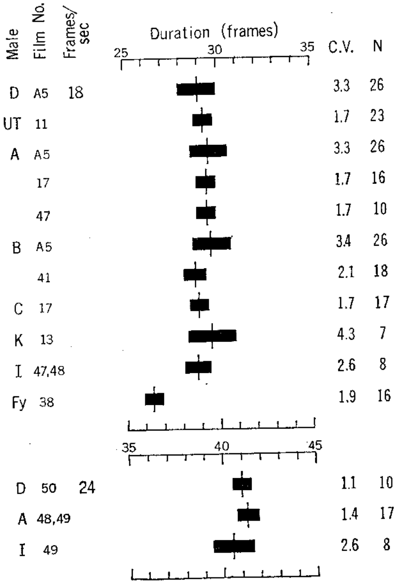

Figure 6. Durations of Struts by individual males, Ford's Creek Lek, 1968. Thin vertical line, mean. Heavy horizontal bar, one standard deviation on either side of the mean. C.V., coefficient of variation (100 × S.D./mean). N, number of measurements. As filming rates were not precisely calibrated, close comparisons between individuals are justified only within the same reel of film or in successive reels filmed at the same speed.

To estimate the stereotypy in the displays of different individuals, I analyzed filmed sequences of this display for a number of individuals. Using a single-frame projector, I determined the number of frames between two distinctive moments in the Strut: the highest point of the sac's first upward excursion (end of Stage IB; Table 1); and the maximum protrusion of the bare membranes just after the first snap (Stage IIIB; Table 1). This interval is slightly shorter than that measured on the galvanometric tracings.

These measurements taken from films were less accurate than those from galvanometric tracings, both because of the inherent uncertainties introduced by the discrete frames and because of the approximate calibration of filming speeds. The discrete frames introduced an experimental uncertainty approaching the reciprocal of the filming speed. A Bolex H16 camera with an internally regulated filming rate was driven by battery-powered electric motor. Variation in the constancy of the filming rate was insignificant. Because the filming rates were not precisely calibrated it is possible that the rate changed slightly whenever the controls were reset. Consequently I analyzed separately each reel of film exposed without changes in the controls for filming rate. A filming rate of about 18 frames/second allowed me to compare as many as 78 Struts by three males on the same reel of film. In 1968 on the Ford's Creek Lek I obtained several suitable films of seven adult males and one first-year male. My measurements from these films are summarized in Figure 6.

These results differ from those obtained from galvanometric tracings in two ways, both explainable on the basis of the uncertainties just described. The slightly higher mean values (about 1.6 seconds) for a slightly shorter interval in the display probably reflect the inaccurate calibration of the filming rate. The higher coefficients of variation (1.1 to 4.3%) presumably represent the additional variation introduced by the discrete frames of the film. These limitations, however, do not affect the conclusion that the different adult males performed their Struts with almost the same temporal patterning.

In spite of the chances of slight differences in filming rates during different reels of film, my measurements revealed no wide divergence in the displays of different individuals (Figure 6). In comparisons between indivi-

TABLE 2

Statistical significance of individual differences in males' Strut displays, Ford's Creek Lek, 1968

					Direction of Difference	
Males Compared	Film No(s).	d.f.	t	P	Mean Strut Duration	Mating Success
B, D	A5	50	2.246	.02-.05	B>D	D>B
A, D	A5	50	1.852	.05-.01	A = D	D>A
A, D	48, 49, 50*	25	1.345	.1-.2		
UT, K	11, 13	28	0.710	.4-.5	UT = K	UT>K
A, C	17	31	2.874	<.01	A>C	A>C
A, I**	47, 48	27	2.390	.02-.05	A>I	A>I
A, I**	48, 49*	23	2.416	.02-.05		
B, Fy**	41, 38	32	11.65	≪.01		

* These sequences were filmed at approximately 24 frames/second; all other sequences were filmed at about 18 frames/second.

** First-year male. All other males were adults.

In the following films each male studied had one or more females within or near his territorial boundary: A5, 11, 13, 17, 41, 47, and 48 (only the part exposed at 18/second).

dual males in the same or closely spaced reels of film, some significant differences in Student's t-tests do appear (Table 2). These slight differences do not have a consistent relationship with the males' successes in mating (Table 2). The males' performances apparently remained consistent on different days and under conditions of different proximities to females. Measurements from my 1967 films give similar results.

In sound spectrograms the acoustic components of the display again showed a high degree of consistency in the performances of any one individual and only slight differences between individuals. Identifiable tape-recordings could be obtained only from the few males nearest my blind. Measurements of the interval between the two snaps in performances by the same male varied no more than 1% on either side of the median value, while the median values for different adult males differed by no more than 4% (Table 3).

TABLE 3

The interval between the two snaps at the culmination of the Strut display

Male	Age	Year	Median (Seconds)	N
C	A*	1968	.190	16
CMP	A	1968	.187	12
B	A	1968	.195	15
13	A	1969	.194	4
Y-1	Fy	1968	.183	7
Y-2	Fy	1968	.186	6
27	Fy	1969	.187	12

Measurements were taken from sound spectograms produced on the same machine within a few days' time. The range of measurements for each male fell within 1% of the median value; the measurements were heavily clustered at the median.

* A, adult; Fy, first-year.

Again, within the limits of my small sample of males, differences in the displays of individual adult males show no consistent relation to mating success. Among the three populations I studied, there are no detectable geographic differences in the acoustic components of the Strut display, a conclusion supported by additional measurements of spectrograms from males that could not be individually identified in my recordings. Thus, in adult male Sage Grouse, the Strut display constitutes a highly complex, yet remarkably stable, coordination.

Peculiarities in Struts by one-year-old males.

The performances of first-year males differ consistently from those of the older males. Their Struts are performed with a quicker tempo, although not with greater variability. In 19 galvanometric tracings of the acoustic output from a first-year male, the mean interval was 72.5 units (1.45 secs) with a standard deviation of 0.56 units (coefficient of variation, 0.8 of one percent). The mean is only about 6% less than the mean obtained for the adult male C (see above), but the ranges obtained for the two males did not overlap (male C, 76-78.5 units; first-year male, 71.5-74 units). Similarly, in the measurements taken from filmed displays one first-year male stands out clearly from the adults (Figure 6, Table 2), although another (Male I) resembles the adults. The quicker tempo of first-year males' Struts was evident even in the field.

Several first-year males in each year of my investigation showed a further abnormality in the temporal patterning of their Struts. These individuals consistently heaved their chest sacs upward three times, rather than twice, before beginning the final phase of compression and release. Older males never had this aberration. A few measurements on films of such abnormal, triple-throw Struts revealed that the timing of the first two excursions of the chest sac conformed to the usual pattern for first-year males. So these abnormal Struts incorporated an additional component into the display without disturbing the durations of the usual components.

In the performances of first-year males, the interval between the two culminating snaps was slightly shorter than in adults (Table 3). Sound spectrograms also revealed that, in the Struts of two of three first-year males, the second coo had an atypical structure. The note was longer than those of adults and included a discontinuity between a rising initial segment and a longer terminal segment.

Variation in the tonal quality of the acoustic components.

In spite of the extreme stereotypy in the temporal patterning of the Strut, there is appreciable variation in the quality of the sounds heard, which seems to depend on the bird's orientation with respect to the listener and on the bird's distance. Normally, the final *poink* sound has a mellow, resonant tone that probably depends on the rising and falling whistle interposed between the two sharp snaps. When this quality is lacking, the final sound becomes a dull *pop*, a difference evident to the human ear. Presumably because the high frequencies of the whistle attenuate faster and in addition are produced with less intensity, the mellow tone in the culminating sound of the Strut never carries more than 100 meters. The snaps and coos, in contrast, can be heard from at least a half kilometer on a still morning. In addition, the whistle responsible for the mellow tone is apparently beamed to the side during the Strut. From distances of 20-50 meters the mellow quality is scarcely perceptible when a Strut is oriented directly toward the listener. Another, less easily noticed, null occurs when a Strut is oriented directly away from the listener. Finally, the mellow quality is noticeably diminished in the Struts of first-year males, regardless of their orientation, and occasionally in the Struts of older males late in the morning. From a listener's standpoint, the tonal features of the sounds accompanying a Strut thus manifest less constancy than do the temporal features.

Variation in intervals between Struts.

Persistence in Strutting varies with the male's distance from females (WILEY, in press), but even when maximally stimulated by females within his territory a male always pauses for several seconds between Struts. The interval between the same point in successive Struts is always at least 4.5 seconds and averages 8-10.5 seconds during continuous Strutting. Successive intervals varied considerably, even when the male's external situation changed little. In uninterrupted sequences of 10-25 Struts, coefficients of variation for the interval between the same point in successive Struts ranged from 9-35% (Table 4).

The large standard deviations render most differences among individual males' mean Strutting rates statistically insignificant. Nevertheless, in 1968 the male responsible for most of the copulations, Male D, often Strutted at lower rates with females in his territory than did his less successful neighbor, Male TM, a difference that I ascribed to Male D's fatigue after a morning

TABLE 4

Variation in intervals between Struts

Film Nos. (Approx. Rate)	Male	Mean ± S.D.	N	C.V.
A5 (18/sec)	D	154.9 ± 29.6*	25	19.1
	A	151.0 ± 15.4	25	10.2
	B	158.9 ± 17.2	25	10.8
11 (18/sec)	UT	179.5 ± 17.5	21	9.8
17 (18/sec)	A	170.0 ± 25.6	15	15.1
	C	160.4 ± 27.1	21	16.9
47, 48 (18/sec)	A	178.7 ± 40.3	10	22.5
	I	170.9 ± 50.4	16	29.5
48, 49, 50 (24/sec)	D	252.9 ± 86.4	9	34.2
	A	238.6 ± 53.0	16	22.2
	I	207.7 ± 31.2	7	15.0

* Number of frames between the same point in successive Struts. Filming rates were only approximately calibrated, so comparisons between individual males are justified only within the same reel of film or in successive reels filmed at the same rate. None of these possible comparisons is statistically significant in Student's t-tests. In the sequences filmed at 18 frames/second, each male had one or more females within or near his territorial boundaries.

of uninterrupted activity (Wiley, in press). In 1967 Male N, who acquired a position in the mating center after the peak of the mating had passed (see Wiley, in press), in the absence of females included short intervals in his bouts of Strutting more often than did four other males, including one that bred as successfully as Male N. My few analyses of first-year males suggest that they resemble older males both in the means and the variability of intervals within their bouts of Strutting.

CONTEXTS

During the height of the season male Sage Grouse on a lek begin almost uninterrupted display each morning just as the eastern sky begins to brighten. Displays are performed at intervals of 6-12 seconds. As the morning progresses the males' activity abates somewhat and becomes more contingent on the proximity of females (Wiley, in press). Nevertheless, even after nearly all females have left for the morning, males still spontaneously begin short bouts of Strutting until they too leave the lek for the day. Again in the evening when the males return to the lek, they engage in bouts of Strutting before any females arrive. Thus, although the proximity of females provides a potent stimulus for Strutting, even when females are distant males will engage in bouts of Strutting.

Especially in the early dawn, a characteristic vocalization of arriving females seems to stimulate Strutting by males. Arriving females often fly over the center of the lek, uttering several *quack* calls, before landing. My observations suggested that these calls stimulated males to begin Strutting, even though no females were nearby on the ground.

Another stimulus for Strutting might emanate from other Strutting males. Early in the morning before females had arrived in numbers, the Strutting activity on a lek sometimes seemed to come and go in waves. After a quiet pause for 15-30 seconds, activity would rapidly crescendo, as if by contagion. Late in a morning's activity, when two neighbors had both remained quiet for some time near each other, if one began to Strut, often the other would begin too. However, even in the absence of any clear external stimulus, a male would periodically initiate a bout of Strutting. As an impetus for the initiation of Strutting, this apparent spontaneity was difficult to separate from the possibility of weak contagion in the Strutting bouts of nearby males.

While on the lek, males normally Strut only within the confines of their territories. During the breeding season, males will sometimes display near females away from any lek. Normally, however, Strutting away from any lek lasts only a short while. Often it occurs temporarily after males and females have been flushed from a lek by a predator (Wiley, in press).

RESPONSES

A Strutting male within his own territory elicits no obvious responses from other males. There is some possibility, discussed above, that Strutting stimulates neighboring males to Strut, but this possible contagion was not quantitatively verified.

Any male will expel other males intruding upon this territory once he notices their presence, but I had little indication that a territorial male's aggression was specifically released by the Strut display. During periods of active mating, young males in Relaxed Posture will often penetrate to the center of the lek in association with females, which they superficially resemble in rear view. Those few intruders that began to Strut within another male's territory were immediately chased across the territorial boundary. Territorial males, however, expel intruding males, once detected, regardless of their posture or activity. By reducing an intruder's chances of escaping detection, Strutting makes attack by the territorial resident more likely.

The presence of a territorial male within his territory clearly does influence the behavior of his neighbors, for if a territory falls vacant one or more neighboring males will move their territories into the vacancy. However, this process is normally a gradual one, often lasting several days (WILEY, in press). Furthermore, the effect of a territorial male on his neighbors might depend largely on his boundary encounters with them. The Strut display thus seems to elicit little in the way of specific, immediate responses from other males. Whether or not a male's Strutting exerts some tonic influence on his territorial neighbors remains uncertain.

Females on the other hand interact closely with Strutting males, especially at the mating center, where the females congregate. Elsewhere within the lek, females usually appear to avoid Strutting males or ignore them (WILEY, in press). At a mating center females gather into a dense pack, adopt a Relaxed Posture, and move primarily to avoid other females and to orient with respect to the Strutting male when he approaches. At close range, females tend to orient obliquely away from the front of a Strutting male. When sufficiently aroused they begin to assume the Sollicitation Posture in similar orientations. A Strutting male at a mating center, therefore, elicits clear responses from the females congregated there, and these responses lead gradually to copulation.

In addition, females might respond to Strutting males in their efforts to locate the mating center within the lek, but the evidence regarding this point remains equivocal (WILEY, in press).

RELATED BEHAVIOR PATTERNS

Two behavior patterns of male Sage Grouse, the Head-jerk and the Intention Strut, seem to be adjuncts of the Strut display. Although no measurements of these brief movements were taken, both appear in the field to have stereotyped form.

Head-jerk (LUMSDEN: Grunt Display; HJORTH: Snoring).

This unprepossessing movement consists of a brief upward rotation of the cranium while the beak opens slightly. Simultaneously, the chest sac twitches a little, and the head jerks backward about 2 cm. A brief sound like a quiet belch is produced during this movement. On frosty mornings, condensing vapor near the bird's beak revealed that a puff of air was expelled, probably from the air sac. HJORTH (1970) incorrectly surmized that the Head-jerk involved inhaling air into the lungs. Earlier workers had also believed that air was swallowed during the Head-jerk in order to inflate the chest sac (PATTERSON, 1952).

A male usually performs one Head-jerk in the interval between two Struts. Often the Head-jerk is omitted, and occasionally two Head-jerks occur between successive Struts. The intervals between the Head-jerk and the preceding and succeeding Struts are positively correlated, but with considerable scatter. Thus the Head-jerk seems incorporated into the Strutting rhythm; a longer interval from Strut to Head-jerk is likely to mean a longer interval from Head-jerk to Strut.

In five samples of at least 20 Strut-Strut intervals from adult males in 1968, the proportion of intervals that included a Head-jerk ranged from 70 to 85%.

Contexts. Males when Strutting at maximal rates with females in their territories seemed to include Head-jerks somewhat more regularly than at other times. I could detect no tendency for Head-jerks to occur principally in agonistic contexts, for instance, preceding territorial boundary disputes or during the close approach of two Strutting males, as LUMSDEN (1968) suggested. Instead, the Head-jerk is apparently an adjunct to the Strut display.

Responses. I could detect no particular responses to the Head-jerk. None of my observations suggested that it had a significant role in intraspecific communication independent of its association with the Strut display.

Intention Strut.

Occasionally a male will perform the initial segment of a Strut without continuing through the entire display. The wings are extended and the body axis tilted upward in front, as if in preparation for the first sac throw, but instead the male returns to the Strutting Posture. One, or on rare occasions two, Intention Struts often preceded the initial full Strut in a bout. The strength of the male's motivation to Strut seemed not to affect the probability of an Intention Strut at the beginning of a bout of Struts. Even a highly motivated male with many females in his territory, after interrupting his displays for a territorial encounter with a neighboring male, would perform an Intention Strut as he resumed his Strutting among the females. Perhaps after a male has completely collapsed his chest sac for other activities, an Intention Strut allows a preliminary inhalation to prime his esophageal sac or lungs before normal Strutting begins. The absence of Intention Struts within a bout of Strutting would be explained if the prime is retained as long as the Strutting Posture is held. No specific responses to the Intention Strut were detected. Like the Head-jerk, the Intention Strut, in both context and responses, seems adjunctive to the Strut display.

DISCUSSION

Variability in other "fixed" action patterns.

The only other attempts to measure the variability in bird's movements during displays, the studies by DANE *et al.* (1959) and by DANE & VAN DER KLOOT (1964) on Goldeneye ducks (*Bucephala clangula*), also revealed little variability in each individual's performances, at least for the species' most stereotyped displays, but individual differences were apparently much greater than I found in Sage Grouse displays. DANE took his measurements from films exposed at 24 frames/seconds. Because he could film any one individual only long enough to obtain a few specimens of each type of display, he presents means and standard deviations for the population as a whole and supplies only ranges for the different individuals. The Goldeneye's two most stereotyped displays had coefficients of variation within the population of 5.1 and 6.1% respectively (DANE *et al.*, 1959). The restricted ranges of the measurements on individual Goldeneyes in comparison to the population range suggest either that the individuals' displays differed appreciably or that an individuals' display tempo varied with time but with some serial correlation over short intervals. The extreme stereotypy in the Strut displays of male Sage Grouse might represent the limit for stereotypy in the actions that comprise avian displays. To confirm this speculation, we shall need more measurements of variability in the displays of other species.

The acoustic production of birds has proved easier to measure, since the advent of the sound spectrograph, than have other manifestations of motor coordinations. In sound spectrograms the durations of short syllables or short twilight from several kilometers. Notwithstanding its importance in broadcasting information about the location and size of a lek, the Strut also figures prominently in close range interactions, particularly between males and females.

The evolution of highly stereotyped signals for use in heterosexual communication apparently depends on the species' mating system. Elaborate displays, and striking plumage, are frequent features of highly polygynous species (Darwin, 1871; Marler, 1956; Sibley, 1957). At least in the polygynous gallinaceous birds, most of these elaborate displays also seem to manifest extreme stereotypy and figure prominently in the male's courtship behavior. The feature of a polygynous mating system that favors the evolution of elaborate, stereotyped signals for heterosexual interactions is probably the unusually brief courtship (Sibley, 1957). In the course of a year, a female Sage Grouse interacts with males primarily during one or two hours on several mornings preceding copulation (see discussion in Wiley, in press). Such species would require unusually salient species-specific signals for use in hetero-sexual communication, in order to ensure that females were aroused by and copulated only with conspecific males. Thus stereotypy in avian displays can subserve at least two purposes in communication: communication at long range; and communication between individuals in transitory, but biologically important, communication with one another. The importance of stereotypy in these situations is clarified by considering the importance of redundancy in communication.

Redundancy can be thought of as patterning in sequences of signals, which the receiver eventually can come to predict. Redundancy will counteract noise in the communication channel or, an equivalent statement, will improve the chances of receiving and correctly interpreting the signal (Shannon & Weaver, 1949; Cherry, 1966). The channel in animal communication is impossible to describe mathematically; in qualitative terms, it includes the medium between the signaler and the recipient. A criterion for the correct interpretation of a signal in an animal communication system is the ensuance of a biologically appropriate response (Marler, 1961). The sources of noise in the channel between two animals include perturbations in the medium, which can introduce variable distortions into the signal during its transit to the receiver, and nonbiological sounds that can mask the signal. Particularly at greater distances these sources of noise increase. In addition, the medium is ordinarily shared by many species for intraspecific communication; the possibility of confusing heterospecific signals with homospecific signals is a further source of noise important in animal communication. Redundancy in the signal can reduce the probability of errors in interpretation as a result of both these sources of noise, but only when the receiver has an adequately long sample of the signal to analyze. Redundancy takes time.

A second way to counteract noise is to encode the signals appropriately. Signals that provide maximal contrasts among themselves and with any patterns inherent in the noise will have less chance of misinterpretation (SHANNON & WEAVER, 1949; CHERRY, 1966). In animal communication channels, particularly the second category of noise mentioned above has considerable inherent patterning. For intraspecific communication species sharing the same channel should thus tend to evolve signals as different as possible from each other (MARLER, 1956, 1960). Coding would have particular importance when only a short time is available for the signaler and receiver to interact, so that sequential redundancy would prove less useful.

Coding and redundancy, however, merge with each other. Coding pertains to the patterning within a signal, redundancy to that in sequences of signals. To distinguish coding from redundancy requires establishing some demarcation in the continuum between components of signals and combinations of signals. In studies of animal communication, one might distinguish each spatial configuration as one signal, so that the distinction between coding and redundancy would relate to a distinction between spatial and temporal patterns; for instance, between the configuration of the male's plumage and the coordination of his display. Yet this simplification is ultimately inadequate; the various components of a spatial pattern are often not perceived simultaneously; and each perception of a spatial configuration, however compact, requires some finite time. Spatial patterns are perceived only in time. No matter how we decide to partition coding and redundancy, in order to minimize the chances for misinterpretation when the time for communication is short, signals should incorporate as much spatial patterning and temporal patterning with short periodicity as possible. The unusual development of these two sorts of species-specific patterning in the Strut display of male Sage Grouse accords with the unusually brief association of the sexes preceding copulation.

The evolution of increasingly efficient coding and increasing redundancy requires larger investments of time and energy by the signaler and greater conspicuousness of the signals to predators as well as conspecifics. The advantages gained in intraspecific communication would eventually be balanced by the loss of time and energy for other activities and the risks of predation.

Different features of Strutting behavior clearly differ in their variability. Intervals between successive Struts fluctuate far more than do the repeated coordinations themselves. The possibility remains that the more variable components of Strutting provide intergrading signals that convey the continuous changes in the male's internal state. I did not detect any differences in the reactions of other birds to differences in a male's Strutting rates. Furthermore, Strutting rates within bouts usually approximated the maximum, so Strutting rates possibly have developed a degree of typical intensity (MORRIS, 1957). The relative constancy of behavioral expression would then fail to reveal, over an appreciable range, the fluctuations in the bird's internal state.

Mechanisms underlying the control of stereotyped behavior.

Any highly stereotyped motor coordination raises questions about its ontogenetic development and physiological control. The Strut display of male Sage Grouse shows extreme developmental stability, as individual differences in performance are slight. The physiological control of the display also shows great stability, because different performances by the same individual vary so little. A stable pattern either in adult physiological or in developmental processes requires the existence of a source for that specific pattern. In either case, this patterned source might include only properties of the central nervous system itself; it might include reafferent feedback from peripheral structures; or it might include environmental patterns exogenous to the animal (see BULLOCK, 1961; KONISHI, 1966; HAILMAN, 1967; HINDE, 1969).

It is now well established that the development of highly stereotyped motor patterns can depend on specifically patterned exogenous information. Instances include complex motor patterns that depend on cultural transmission, as do the song patterns of certain passerines (THORPE, 1961; MARLER, 1970b; NOTTEBOHM, 1970). Culturally transmitted patterns often, perhaps inevitably, vary geographically. The absence of any indication of geographical variation in the Strut display of Sage Grouse is circumstantial, but by no means conclusive, evidence that this characteristic rhythmical coordination would develop in the absence of any exposure to normal Struts performed by other individuals.

If development does proceed normally in the absence of specific exogenous stimuli, the patterning in the central nervous system must derive from patterns in sequential ontogenetic processes that derive ultimately from patterns in the individual's genes. This endogenous development of central nervous patterning might still depend on the patterns in proprioceptive feedback that result from the physical properties of moving anatomical structures. Such a possibility seems particularly feasible in the case of the Sage Grouse Strut, a coordination that involves rhythmical movements of relatively massive, components of Strutting provide intergrading signals that convey the continuous changes in the male's internal state. I did not detect any differences in the reactions of other birds to differences in a male's Strutting rates. Furthermore, Strutting rates within bouts usually approximated the maximum, so Strutting rates possibly have developed a degree of typical intensity (MORRIS, 1957). The relative constancy of behavioral expression would then fail to reveal, over an appreciable range, the fluctuations in the bird's internal state.

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In this model, an important component of the developmental process would remain within the central nervous system: a predisposition to adopt the specific efferent pattern that generated the maximum amplification ratio in the moving structure. The central nervous system need not include a fully formed "template" of the final coordination. Instead, it would require an endogenous cybernetic mechanism to maximize one specific property of the reafferent feedback. Stability of C.N.S. development would then depend in part on stability in the development of gross anatomical structures, and in part on stability in the development of specific C.N.S. properties. It seems plausible that the central nervous system could exhibit canalized development as pronounced as that possible in other anatomical systems. If such a system did operate in the ontogeny of a stereotyped action pattern, then the variability of this action pattern within a population could approach the morphological variability characteristic of the population. This condition, although not convincing evidence for the harmonic reafference model, is confirmed by my analysis of the Strut display of Sage Grouse. Because many avian displays, as well as locomotor patterns, involve significant movements of anatomical parts, the harmonic properties of these moving structures might often influence, through proprioceptive feedback, the development of central nervous patterning.

Proprioceptive feedback dependent on the harmonic properties of moving structures might also promote stability in the immediate control of a stereotyped action pattern. However, two delays are interposed between the efferent and the reafferent signals. First, the reafference lags a slight amount owing to the finite conduction time in the peripheral nerves. This lag, however, might be slight compared to the lag between the impressed force and the harmonic response. This lag increases as the impressed frequency increases, and it reaches 90° when the impressed frequency, ω_i, equals the natural harmonic frequency, ω_n, of the moving structure. Under conditions of friction that allow significant amplification ratios, the maximum amplification is produced by frequency ratios, ω_i/ω_n, between 0.5 and 1.0 (Wylie, 1960). So the impressed force might lead the displacement of the peripheral structure by a substantial fraction of a cycle. Reafference in these circumstances could only influence the efferent pattern for a succeeding cycle. Such considerations suggest that studies of the temporal patterns and variability of muscle contractions during stereotyped displays might improve our understanding of their control. Just as in the model proposed for the ontogeny of central nervous patterning in response to reafferent feedback, the central nervous system would require an endogenous comparator to assess the reafference in terms of some goal, such as maximum amplitude multiplication.

Patterning inherent in proprioceptive feedback, dependent on the harmonic properties of moving anatomical structures, might thus allow the nervous system both to tune its output in the course of development and then allow maintenance tuning in the adult. Variability in repeated performances of the same individual might then reflect either a residual uncertainty in the central efference or slight differences in the mass and elasticity of the anatomical structure, perhaps as a result of changes in tissue fluids.

Peculiarities in the displays of first-year males.

The distinctive features of the young males' displays add some evidence that the tempo of the display depends on the morphology of the chest region. First-year males performed their Struts with a quicker tempo: the durations of their Struts were slightly shorter than those of older males, and the interval between the two snaps in the culmination of the display was also slightly shorter.

The esophageal sacs of young males, at least until relatively late in the breeding season, remain noticeably smaller than those of older males (Patterson, 1952; Dalke *et al.*, 1963; Wiley, in press). In addition, first-year males' chests appeared less elastic. No accurate measurements of chest-sac dimensions are available for young males, but my impressions in the field suggested that the sacs of young males increase in size during the breeding season and do not reach maximal sizes until after the peak of the breeding (Wiley, in press). Some limited experiments have suggested that growth of the chest sac depends on testosterone levels (Clarke *et al.*, 1942). As the testes of young males reach their maximal volumes late in the breeding season (Eng, 1963), the fullest development of their chest sacs should also occur later than in older males. Although I have no measurements that allow a comparison of the same individual first-year male earlier and later in the season, the quicker tempo of the young males' Struts was especially apparent early in the season, when the smaller size of their chest sacs was also most apparent.

The differences in the size and resilience of the young males' chest sacs seem to accord with the shorter period of their oscillations. When a year-old male added a third cycle of inflation before the culmination of the display, the tempo of the sac's excursions did not change. Further evidence that the less developed chest sacs of young males determine the timing of their performances comes from the low coefficients of variation for the durations of each individual's Struts. First-year males' performances, so far as my limited measurements can indicate, have no more variable displays than do older males. If we suppose that the peculiar displays of immature males resulted from incompletely crystallized neural mechanisms, then we would expect the performances of young males to exhibit greater variability. Certain displays of young male Goldeneyes apparently do manifest greater variability than the action patterns of older males (Dane *et al.* 1959). Hence, in this species certain displays of immatures seem controlled by incompletely stabilized neural mechanisms. In contrast, young male Sage Grouse appear to have fully stereotyped display rhythms in accordance with the anatomical characteristics of their chest sacs.

SUMMARY

The Strut display of male Sage Grouse, *Centrocercus urophasianus*, exemplifies a complex "fixed" action pattern. The display results in the inflation of the male's large esophageal sac, which is then used to produce a strange sound that includes two sharp snaps 0.19 seconds apart. Measurements of the durations of an individual's displays usually yielded a coefficient of variation (C.V.) less than 4%; the most accurate measurements had C.V.'s less than 1%. The intervals between Struts, in contrast, had much higher variability. No geographic differences were detected among three populations in Wyoming and Montana. Nor did the slight differences in the displays of individual adult males have a consistent relation to their successes in mating. First-year males performed their Struts with faster tempo but not with greater variability.

The temporal stereotypy in the Strut display approximates or exceeds the stereotypy in passerine songs. Stereotyped motor patterns in vertebrates often subserve communication at long range or between individuals in brief, but biologically crucial, contact with each other. The Strut display exemplifies both of these functions in communication. Stereotyped, complex signals incorporate more redundancy and/or more efficient encoding; they thus enhance the receiver's chances of detecting and correctly interpreting the signal.

Reafference that depends on the harmonic properties of moving structures might help to explain both the developmental and physiological stability of this stereotyped motor coordination. Because year-old males' displays show no greater variability than those of older males, the peculiarities of young males' performances probably are not the result of incompletely crystallized neural mechanisms.

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ZUSAMMENFASSUNG

Das Stolzier-Verhalten der Männchen von *Centrocercus urophasianus* veranschaulicht ein komplexes „fixiertes" Verhaltensmuster. Dieses Verhalten resultiert im Aufblähen des weiten Oesophagussackes des Männchens, mit dem dann ein eigenartiger Laut produziert wird, der zwei scharfe Schnalzlaute im Abstand von 0.19 sek. beinhaltet. Messungen der individuellen Verhaltensdauer ergaben gewöhnlich einen Variations-koeffizienten (C.V.) geringer als 4%. Die genauesten Messungen lieferten einen C.V. unter 1%. Im Gegensatz dazu zeigen die Intervalle zwischen dem Stolzieren eine wesentlich grössere Variabilität. Zwischen drei Populationen in Wyoming und Montana konnten keinerlei Unterschiede gefunden werden. Die geringen individuellen Unterschiede im Verhalten adulter Männchen liessen ausserdem keine konsequente Beziehung zu deren Erfolg hinsichtlich der Paarung erkennen. Männchen im erstem Jahr ihrer sexuellen Reife vollführen das Stolzieren schneller, jedoch ohne erhöhte Variabilität.

Die zeitliche Stereotypie des Stolzier-Verhaltens ist annähernd gleich gross wie oder grösser als die Stereotypie im Gesang der Passeriformes. Bei Vertebraten dienen stereotype motorische Muster oft der Verbindung auf lange Sicht oder dem kurzen, biologisch jedoch wichtigen Kontakt zwischen Individuen. Das Stolzier-Verhalten veranschaulicht beide Funktionen. Stereotype, komplexe Signale beinhalten mehr Ueberfluss an Koden und/oder nützlichere Koden; auf diese Weise vergrössern sie die Möglichkeit des Empfängers, das Signal zu entdecken und korrekt zu interpretieren.

Eine Reafferenz, die von den harmonischen Eigenschaften der anatomischen Strukturen abhängt, könnte zur Erklärung sowohl der Stabilität während der Entwicklung als auch der physiologischen Stabilität herangezogen werden. Da das Verhalten junger Männchen keine grössere Variabilität als das älterer Männchen zeigt, sind die Besonderheiten im Verhalten der jungen Männchen wahrscheinlich nicht auf unvollständig herauskristallisierte neurale Mechanismen zurückzuführen.