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COURTSHIP ETHOLOGY OF CAROLA'S PAROTIA (*PAROTIA CAROLAE*)

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ABSTRACT.—Detailed descriptions of behavior patterns are a major objective of ethology, because they serve as the basis for identifying the elements that constitute the behavioral component of the phenotype. In regard to avian courtship displays, the lack of detailed studies has limited the scope of modern ethological investigations. Recent advances in video technology have greatly improved the ability to analyze complex avian behaviors. I examined the ethology of courtship and mating in Carola's Parotia (*Parotia carolae*) using a modern approach intended to facilitate incorporation into existing bioinformatics databases. The questions addressed are as follows. (1) What are the courtship and mating behaviors of wild Carola's Parotias? (2) How are these behaviors structured? And (3) what are the units that constitute complex patterns of behavior? I used digital video to thoroughly characterize two wild populations of Carola's Parotias in Papua New Guinea. The results present a detailed picture of the species' complex courtship ethology, including description of 20 behaviors and the lower-level structure (or "anatomy") of male displays, which alone comprise 58 distinct elements. The modular nature of displays is demonstrated through instances in which various units and subunits are used recurrently, differentially employed, and added or deleted. *Received 1 November 2004, accepted 4 January 2006.*

Key words: bird of paradise, Carola's Parotia, display behavior, ethology, hierarchical organization, modularity, ontology, Paradisaeidae, *Parotia carolae*.

Etología del Cortejo en Parotia carolae

RESUMEN.—Realizar descripciones detalladas de los patrones de comportamiento es uno de los objetivos principales de la etología, pues estas descripciones pueden servir como base para identificar los elementos que constituyen el componente conductual del fenotipo. Con respecto a los despliegues de cortejo de las aves, la carencia de estudios detallados ha limitado el enfoque de las investigaciones etológicas modernas. Los avances recientes en la tecnología de video han mejorado sustancialmente nuestra habilidad para analizar comportamientos complejos de las aves. En este estudio, examiné la etología de cortejo y apareamiento de *Parotia carolae* empleando un enfoque moderno diseñado para facilitar la incorporación de información existente en bases de datos bioinformáticas. Las preguntas abordadas fueron las siguientes: (1) ¿Cuáles son los comportamientos de cortejo y apareamiento de individuos silvestres de la especie *P. carolae*? (2) ¿Cómo están estructurados esos comportamientos? (3) ¿Cuáles son las unidades que constituyen los patrones complejos de comportamiento? Utilicé videos digitales para caracterizar exhaustivamente dos poblaciones silvestres de *P. carolae* en Papua Nueva Guinea. Los resultados presentan una descripción detallada de la compleja etología de esta especie, incluyendo descripciones de 20 comportamientos y la estructura a un nivel

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fino (o "anatomía") de los despliegues de los machos, que por sí solos comprenden 58 elementos distintos. La naturaleza modular de los despliegues es demostrada mediante instancias en las que varias unidades y subunidades son empleadas de forma recurrente, empleadas diferencialmente y añadidas o eliminadas.

DESCRIBING THE BEHAVIORAL component of the phenotype is a major objective of ethology and the foundation on which the comparative study of animal behavior is built (Lorenz 1941, Tinbergen 1959, van Tets 1965). Descriptions that depict behavior patterns at various levels of integration and hierarchical organization are important for understanding the "anatomy" of complex behavioral traits (Tinbergen 1951). Such detailed descriptive work is important for research on the evolutionary origins and patterns of transformation for complex traits like avian courtship displays, because it systematically dissects the phenotype into discrete units suitable for analysis (Schenkel 1956, Eibl-Eibesfeldt 1970).

Although ornithology played a pivotal role in the early development of ethology (Huxley 1966, Lorenz 1966), modern descriptions of complex bird behavior designed for use in comparative evolutionary studies are rare. Most recent research has either reanalyzed data from the classic literature or relied on a patchwork of new and old data collected with vastly different standards and methodologies (e.g., Prum 1990, Paterson et al. 1995, Kennedy et al. 1996, Slikas 1998, Johnson 2000). Progress has slowed, because new data are sparse and few advances have been made toward using the new technologies, concepts, and methodologies available to modernize the process of creating descriptive material explicitly designed for the needs of evolutionary ethology.

Recently, several advances in methodology have greatly improved how behavioral data can be collected, organized, studied, and disseminated. These innovations have only begun to be applied to studies of complex bird behavior. Improvements in video technology include not only recording ability, but also analysis of video using personal computers, enhanced digital-media storage capabilities, and the ability to stream video over the internet. Another innovation is the use of ontologies to represent, archive, and disseminate biological data. "Bio-ontologies" are exceptionally good for formalizing complex areas of biological knowledge; they depict, in a conceptually clear way, the interrelationships and hierarchical structure among the components of

complex systems (Bard 2003, Bard and Rhee 2004). Applying these advances to traditional methods of behavioral description will greatly facilitate widespread dissemination of ethological data, promote new methods of analysis, and encourage integration of knowledge from related fields.

The Carola's Parotia (*Parotia carolae*), a bird of paradise, inhabits the densely forested middle elevations of the western two-thirds of New Guinea's mountainous interior (Frith and Beehler 1998). Birds of paradise exemplify the extreme degree to which phenotypic complexity can evolve as a result of intense selection on courtship signals (i.e., plumage ornaments and displays) and are therefore excellent subjects for examining the evolution of courtship-based phenotypic complexity. However, study is impeded by a lack of high-quality primary data characterizing this complexity. For example, the species in the genus *Parotia* are known to have relatively complicated courtship displays (Gilliard 1969, Schodde and McKean 1973, Frith and Frith 1981, Pruett-Jones and Pruett-Jones 1990, Frith and Beehler 1998), but most species are poorly known at the level of detail needed for comprehensive comparative study. Carola's Parotia, for instance, is the most widespread species in the genus *Parotia*, but virtually all knowledge of its courtship and mating behavior comes from an account of two captive birds and several brief, and clearly incomplete, observations of wild birds (Gilliard and LeCroy 1961, Frith 1968, Frith and Coles 1976, Cooper and Forshaw 1977, Healy 1980, Coates 1990). Modern descriptive studies are needed that clearly depict the anatomy of all components that constitute the courtship phenotype.

The purpose of the present study was to examine the ethology of courtship and mating in the classic tradition, but using a fully modern approach. My goal was not only to describe the courtship behavior of Carola's Parotia, but also to systematically compile a detailed representation of the behavioral components of courtship and mating. The main questions addressed were as follows. (1) What are the courtship and mating behaviors of wild Carola's Parotias? (2) How

are these behaviors structured? And (3) what are the units that constitute complex patterns of behavior? To address these questions, I recorded the courtship behavior of *Carola's Parotia* in multiple formats: text descriptions, digital photo-ethograms from video frame-captures, schematic diagrams depicting the levels of hierarchical organization and integration among components, and permanently archived, web-accessible video clips as vouchers for reference and re-evaluation. Diagrams depicting the hierarchical relational structure of components and video voucher clips are specifically designed to facilitate the transition of ethological data into a modern bioinformatics framework. The overarching goal, however, is to provide effective descriptions of the behavioral components of courtship that will facilitate examination of the phylogenetic underpinnings of the complex and unusual behaviors for which the birds of paradise are renowned.

METHODS

The ethology of *Carola's Parotia* courtship and mating was studied in the wild from two localities in Papua New Guinea (PNG) (Fig. 1). One site was the Mekil Biological Research Station at ~1,700 m above sea level on the southern slope of Mt. Stolle, Sandaun Province; 04°48.803'S, 141°39.176'E. Field work at this site was done from 27 September to 27 October 2000 and from

10 October to 3 November 2003. The second site was a small camp 6 km north of the Herowana village airstrip in the Crater Mountain Wildlife Management Area, at ~1,500 m above sea level, on the eastern flanks of Crater Mountain, Eastern Highlands Province; 06°36.120'S, 145°11.649'E. Field work at this site was done from 13 November to 10 December 2000 and from 12 to 23 December 2001.

To capture and preserve the details of courtship ethology on digital video, local field assistants were employed to search the forest to find terrestrial display territories of adult males and to build observational blinds. From blinds, video recording of unmarked birds was typically done from 0530 to 1030 hours and from 1330 to 1730 hours. Video recording was done with a Sony DCR-VX2000 miniDV digital video recorder using both interlaced and non-interlaced recording formats. All video footage was imbedded with a date and time stamp. At Mt. Stolle, 95 h of observations were made, resulting in >210 min of usable video data. At Crater Mountain, 92 h of observations were made, resulting in >590 min of usable video data.

Deconstructing the major components of courtship ethology into different levels of integration and hierarchical organization is a multistage process. In the first stage, unedited video was imported from tape into a Macintosh computer and stored on the hard drive using Apple iMOVIE2 and iMOVIE3 software. Next,

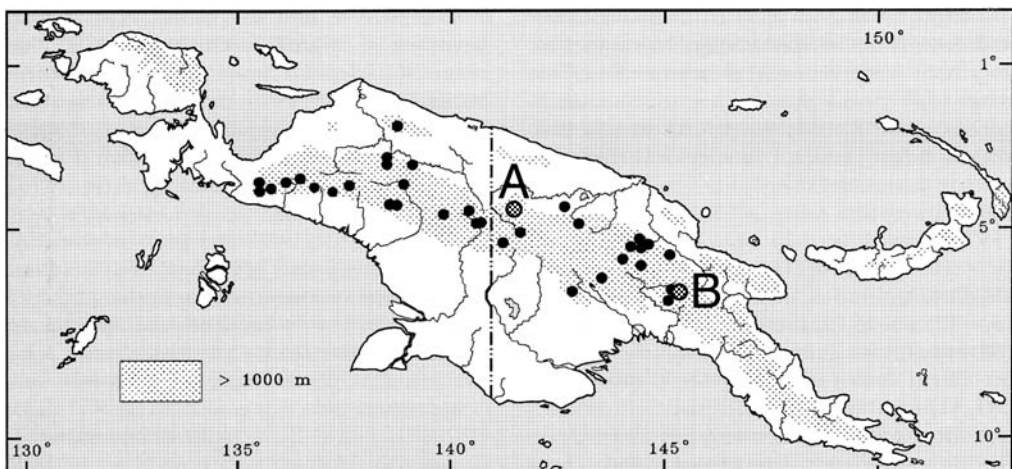


FIG. 1. Distribution of *Carola's Parotia* in New Guinea. Highland areas above 1,000 m are shaded. Solid circles represent known localities, and open circles represent the two study populations: (A) Mt. Stolle, (B) Crater Mountain. Modified from Frith and Beehler (1998).

raw footage was carefully reviewed so that major behavior patterns could be identified. Once identified, each example of a behavior pattern was extracted and divided into individual clips that could be labeled, sorted, and analyzed independently. Individual clips representing major behavior patterns were then carefully reviewed at normal and frame-by-frame playback speeds to identify subcomponents. Finally, each behavior and its component structures were described, and some aspects quantified. Acoustic components were exported from video and imported into RAVEN, version 1.0 (Charif et al. 2003), for analysis.

To examine and depict the relational structure of the components of courtship ethology in Carola's Parotia, I constructed and visualized a simple ontology through a series of schematic diagrams (directed acyclic graphs). The purpose of these diagrams is to depict, in a conceptually clear way, the integration of units described in the study and their interrelationships at different levels of organization. The ontology format used here serves two important functions: (1) it organizes a complex knowledge structure in a form that can be modified and updated more efficiently than traditional descriptions, and (2) it formats the data so that it can be incorporated more readily into existing informatics databases (Bard 2003).

Text descriptions used here are simplified versions of traditional behavioral descriptions. Most accounts include a brief generalized summary of the behavior, followed by a technical record of action patterns. However, some extremely simple behaviors are described with simple summaries only. Included with the general summary are numerical tallies of the component elements of each major behavior and a review of substructure (if any). Macaulay Library catalogue numbers are also given for voucher clips (see below). The second segment of text descriptions includes a more detailed ethological description divided into five sections. The first section, Place, describes where the primary action pattern happens (e.g., horizontal perch or court floor); it also includes placement in relation to other individuals. Next is Posture, which describes general body orientation and lists the relative positions of head, wings, legs, tail, and ornaments. The primary section, Action Patterns, follows; it describes primary body, appendage, and ornament motions.

The next section is Spatial Movement, which describes changes in spatial position during the behavior (e.g., lateral movement along perch). The final section, not relevant to all behaviors, is Other Action Patterns; it lists any other action patterns that are a part of the behavior but that have been described elsewhere—usually displacement behaviors. If a section is not relevant to a specific behavior, it is omitted.

Sequences depicting behavioral changes over a given time frame are illustrated with photographic ethograms derived from video frame-captures. Ethogram construction involved a three-step process. First, a video clip clearly depicting the major components of the behavior was selected, and individual frames were exported as digital images (e.g., jpeg files). Next, the sequence was edited down to a smaller subset of images that best depict the range of motion and action patterns. Images were then enhanced with PHOTOSHOP (Adobe, San Jose, California) to improve clarity. The enhancement process involves color correction, brightness and contrast adjustment, and removal of digital compression and video artifacts. In only one instance was an image modified to digitally remove a distracting background feature (an ill-placed twig). No alterations beyond those described above were made. Finally, the image sequence was arranged in a temporal sequence and annotations (e.g., arrows, point-of-reference lines, etc.) were added.

The last method used to depict the ethology of courtship and mating was permanent archiving of video specimens in the collections of Macaulay Library at the Cornell Laboratory of Ornithology, Ithaca, New York. The purpose of these video vouchers is to provide unaltered ("raw") material as a reference for verification of the courtship ethology described here and to facilitate further study. The entire video data set used in the analysis has been accessioned, with individual clips used as reference vouchers; these are freely available online (see Acknowledgments).

RESULTS

ORNAMENTAL PLUMAGE

Most male courtship displays employ specialized ornaments specific to the genus *Parotia*; therefore, brief descriptions of male ornamental plumage are provided to facilitate interpretation of behavior (Table 1). Figure 2

TABLE 1. Ornamental plumage terminology. See Figure 2 for location of each ornament.

Terms	Definitions
(A) Head wires	Three wire-like feathers with spatulate tips that emanate from behind each eye; called "occipital plumes" by Frith and Beehler (1998).
(B) Nuchal bar	Narrow horizontal bar of highly iridescent blue-green feathers on the rear crown.
(C) Frontal crest	Complex arrangement of feathers covering the top of the head and forehead. It is composed of three distinct parts: supranarial tufts, forehead tufts, and loreal tufts. At rest, forehead and supranarial tufts lay nestled between the loreal tufts. Called "forehead tufts" by Gilliard (1969) and "frontal feathering" by Schodde and McKean (1973).
(C1) Supra-narial tufts	Term used by Schodde and McKean (1973) for the feathers of the frontal crest that emanate from a ridge above the nares, partially concealing the culmen. Note: the adjectival form of "nare" is "narial," rather than "narial" as used by Schodde and McKean (1973).
(C2) Forehead tufts	Coppery bronze erectile feathers of the frontal crest that emanate from the base of the culmen and protrude above the supranarial tufts. Called "forehead crest" by Schodde and McKean (1973), but modified here to avoid confusion with the more inclusive term "frontal crest."
(C3) Loreal tufts	Elongate black feathers of the loreal region with white tips that curve inward over the top of the head, concealing the supranarial and forehead tufts.
(D) Whiskers	Long, wispy feathers that arise from the chin and upper throat. Length and color of these feathers varies among taxa.
(E) Breast shield	Patch of large, iridescent, bronzy green feathers on the upper breast.
(F) Flank plumes	Highly modified contour feathers that emanate from the sides of the upper breast and extend beyond the lower torso. Forms the "skirt" used in the ballerina dance display.
(G) Mantle cape	Plush feathers of the upper back.

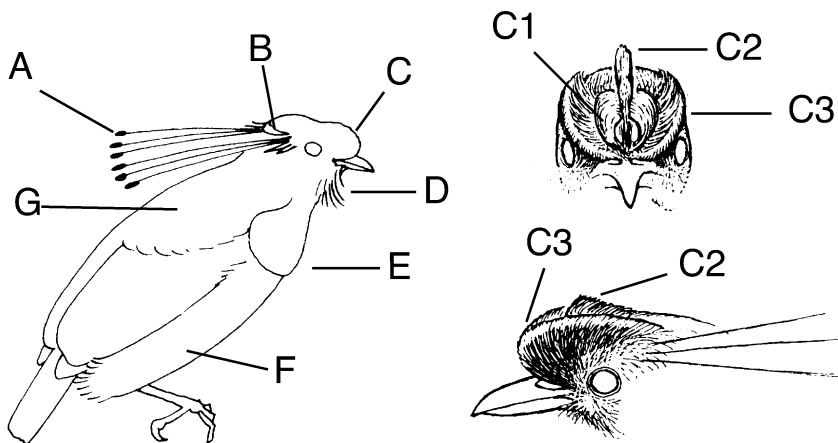


FIG. 2. Specialized plumage ornaments (see Table 1 for descriptions): (A) head wires, (B) nuchal bar, (C) frontal crest, (C1) supranarial tufts, (C2) forehead tufts, (C3) loreal tufts, (D) whiskers, (E) breast shield, (F) flank plumes, and (G) mantle cape. Modified from Frith and Beehler (1998) and Schodde and McKean (1973).

illustrates anatomical locations of ornaments. Comprehensive plumage descriptions have been provided elsewhere (Frith and Beehler 1998).

DISPLAY TERRITORIES AND LEK ORGANIZATION

Males construct and maintain small terrestrial territories, or display courts, used exclusively for courtship. Courts range in area from about 1.0 to 5.0 m². Display courts were cleared of leaf litter and forest debris, except for a thick mat of dark grayish-brown, rootlet-like epiphytic fungi placed on the court by the court owner. All courts had at least one horizontal perch, herein called the "main court perch," which spanned the length of the central portion of the court. Main court perches ranged in elevation from about 0.5 m to >1 m above the court floor, and in diameter from about 1 to 8 cm. Main court perches were used by males when displaying and by females when observing males; males prune leaves from larger branches immediately overhanging the display court.

Lek structure is dispersed; courts appear to be solitary but are within auditory range of one another. All courts within the studied leks were not located; therefore, nearest-neighbor distances were not calculated. Because of the great distances between some courts (in some cases, >1 km), it seems likely that each study site encompassed more than one lek.

VOCALIZATIONS AND SONATIONS

Advertisement vocalizations were heard often during observation sessions. Vocal recordings revealed significant disparity in male advertisement vocalizations between the two study populations. At Mt. Stolle, the advertisement call is a loud, powerfully whistled, three-note "kwoi-kwoi-eeeng" heard throughout the day (Fig. 3A; Macaulay Library Sound and Video Catalog, video no. 21666). In addition, a two-note "kwoi-kweer" and four-note "kwoi-kwoi-kwoi-kweer" were occasionally heard. All "kwoi" notes analyzed consist of a modulated fundamental tone accompanied by all integer harmonics (Fig. 3A). Notes are 0.196 ± 0.016 s in duration, with frequency modulation ranging from a mean low of 1.43 ± 0.04 kHz to a mean high of 2.69 ± 0.32 kHz ($n = 6$). The third note in the three-note call—the "eeeng"—is a pure tone accompanied only by even integer harmonics. The third note lasts

0.148 ± 0.037 s ($n = 3$), with a mean fundamental frequency of 1.97 ± 0.04 kHz ($n = 3$).

At Crater Mountain, the advertisement call is a single, loud, whistled "kwa-a-a-a-ng" that has a frantic or urgent quality to it (Fig. 3B; video no. 21667). The call begins as a pure tone and then changes into an oscillating quaver (Fig. 3B). It has a fundamental tone ranging from a mean low frequency of 1.63 ± 0.03 kHz to a mean high frequency of 3.33 ± 0.21 kHz ($n = 5$) accompanied by all integer harmonics. The mean duration of the call is 0.385 ± 0.011 s ($n = 5$).

In addition to advertisement calls, males of both populations give a diversity of short chips, squeaks, and chortles, some of which may be crude mimicry of other birds and possibly micro-hylid frogs.

In addition to vocal sounds, a conspicuous wing-rattle sonation, or nonvocal sound (*sensu* Bostwick and Prum 2003), is produced. Frame-by-frame analysis of video did not reveal the mechanism of sound production, but supported a one-to-one correspondence between the number of wing beats and the number of rattle sounds emitted. The possibility of the sound being a series of bill-snaps was ruled out, because on several occasions, the displaying bird was holding a leaf in its bill while performing a charge display that produced rattle sounds.

COURTSHIP AND MATING BEHAVIORS

Behaviors used in the context of courtship and mating are described below, beginning with the female component, followed by the male component. Figure 4 summarizes the higher-level organizational structure. Figures 5–7 depict the lower-level organizational structure.

Court visitation.—A female nondisplay mate-searching behavior (Fig. 4). It involves a range of activities in which the visiting female moves among perches, inspects the court floor, inspects the male (when not displaying), and searches for court objects. (Voucher clip: video no. 21668.)

Object gathering.—A female nondisplay mate-sampling behavior (Fig. 4). Objects (placed by the male, see below) are collected from the court floor (held in the bill) and carried away (Fig. 8A). (Voucher clip: video nos. 21669 and 21670.)

Display observation.—A female nondisplay mate-sampling behavior (Fig. 4). While a male displays below, the female looks on from the main court perch and closely follows the

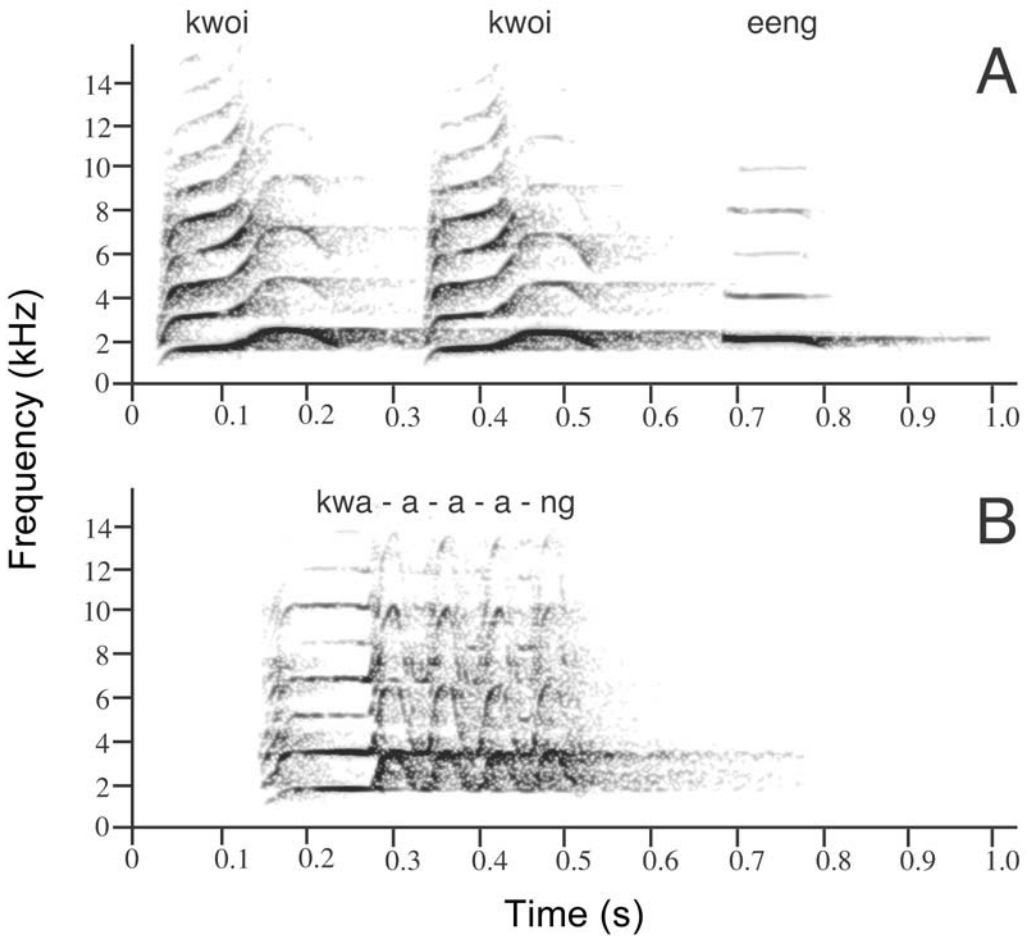


FIG. 3. Sonograms of vocalizations from the two study populations: (A) three-note call from Mt. Stolle (video no. 21666), (B) single quaver from Crater Mountain (video no. 21667).

movements of the male (Fig. 8B). (Voucher clip: video no. 21671.) Place: horizontal perch. Posture: body upright and horizontal (head down or tail down). Action patterns: 180° hop-turns; lowering head to perch (peering between legs); tilting head side-to-side; raising up; turning head (to “look over shoulder”); erecting feathers behind eyes and back of head; ruffling plumage. Spatial movement: lateral movement along perch.

Wing shivering.—A female solicitation display (Fig. 4). While intently observing male display from the main court perch, the female opens her wings slightly and slowly twitches them (Fig. 8B). (Voucher clip: video no. 21672.) Place: horizontal perch above or adjacent to a displaying male. Posture: body horizontal; wings partially open. Action patterns: turning head (away from

male); twitching wings (primaries expanding and shutting); erecting feathers behind eyes and back of head slightly.

Upward bill-point sway.—A female solicitation display (Fig. 4). While perched on the main court perch, the female lowers her head beneath the perch and then raises it, with bill pointing up, while swaying her head side-to-side as if pecking at the air above (Fig. 9A, B). (Voucher clip: video no. 21673.) Place: horizontal perch above displaying male. Posture: body horizontal (head down, tail down); body upright (head up, tail down). Action patterns: lowering head (beneath perch); raising up; outstretching neck; pointing bill upward; swaying head side-to-side (“pecking” at the air). Other action patterns: wing shivering.

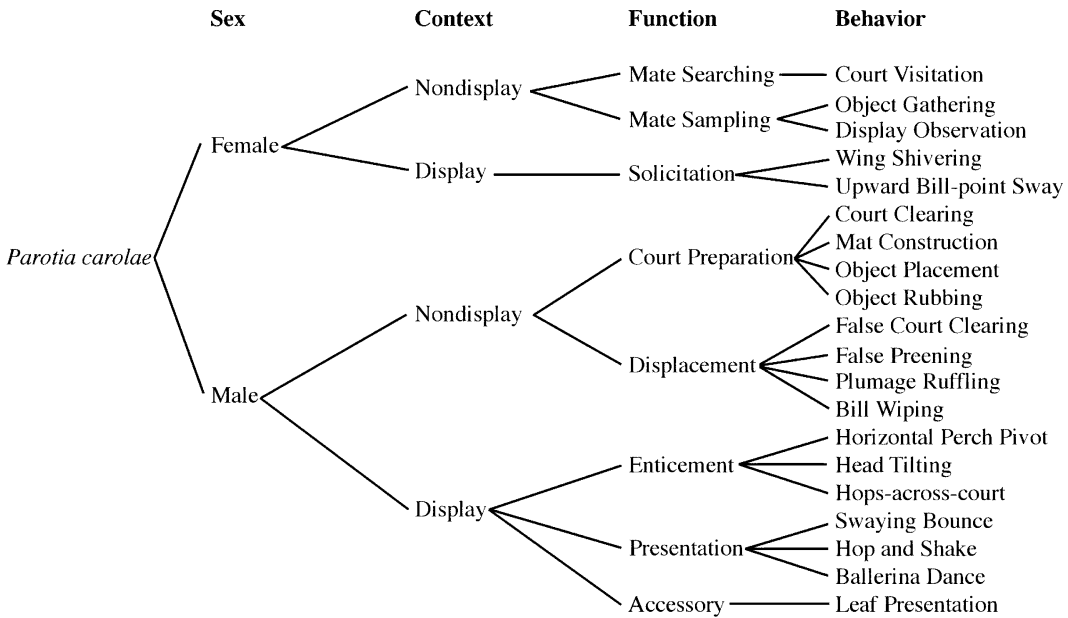


FIG. 4. A schematic diagram depicting the higher-level organizational structure for all 20 courtship and mating behaviors described in the present study.

Court clearing.—A male nondisplay court-preparation behavior (Fig. 4). A range of activities in which leaves, leaf litter, or other forest debris are removed from the court floor. (Voucher clip: video no. 21674.)

Mat construction.—A male nondisplay court-preparation behavior (Fig. 4). Clumps of rootlets or rootlet-like fungus are carried to the court, pulled apart with the bill, and spread around the court floor, forming a dense mat-like layer over the exposed substrate (Fig. 10A). (Voucher clip: video no. 21675.)

Object placement.—A male nondisplay court-preparation behavior (Fig. 4). Small objects (e.g., yellow leaves, mammal fur, snake skin, and soil-dung clods) are carried to the court in the bill, placed on the periphery, and not removed during bouts of court-clearing. (No voucher clip.)

Object rubbing.—A male nondisplay court-preparation behavior (Fig. 4). Court objects, usually leaves or soil-dung clumps, are held in the bill and rubbed back and forth along the main court perch or sapling (Fig. 10B). (Voucher clip: video no. 21676.)

False court clearing.—A male displacement behavior (Fig. 4) similar in form to court clearing. The head is lowered to the ground as if pecking at the ground to remove minute debris,

but the bill does not always touch the substrate, and nothing is actually moved or cleared from the court. (Voucher clip: video no. 21677.)

False preening.—A preen-like male displacement behavior (Fig. 4), in which the male appears to be pecking at feathers along the breast, flanks, and under the wing, but the bill does not touch the feathers. (No voucher clip.)

Plumage ruffling.—A male displacement behavior (Fig. 4). Ritualized ptilo-erection of the contour feathers of the torso. Feathers are puffed and lifted away from the skin with a ruffling and slight shaking motion. (Voucher clip: video no. 21678.)

Bill wiping.—A male displacement behavior (Fig. 4). A ritualized motion, in which the bill is wiped back-and-forth in rapid succession along the perch or against the stems of saplings growing within the court. (Voucher clip: video no. 21679.)

Horizontal perch pivot.—An enticement display from the beginning of the display sequence (Fig. 4). A left-and-right rotation, in place, on the main court perch, with white flank plumes flared conspicuously to the sides (Fig. 11A, B). (Voucher clip: video no. 21680.) It comprises six elements (Fig. 5A). Quantified components are summarized in Table 2. Place: horizontal perch.

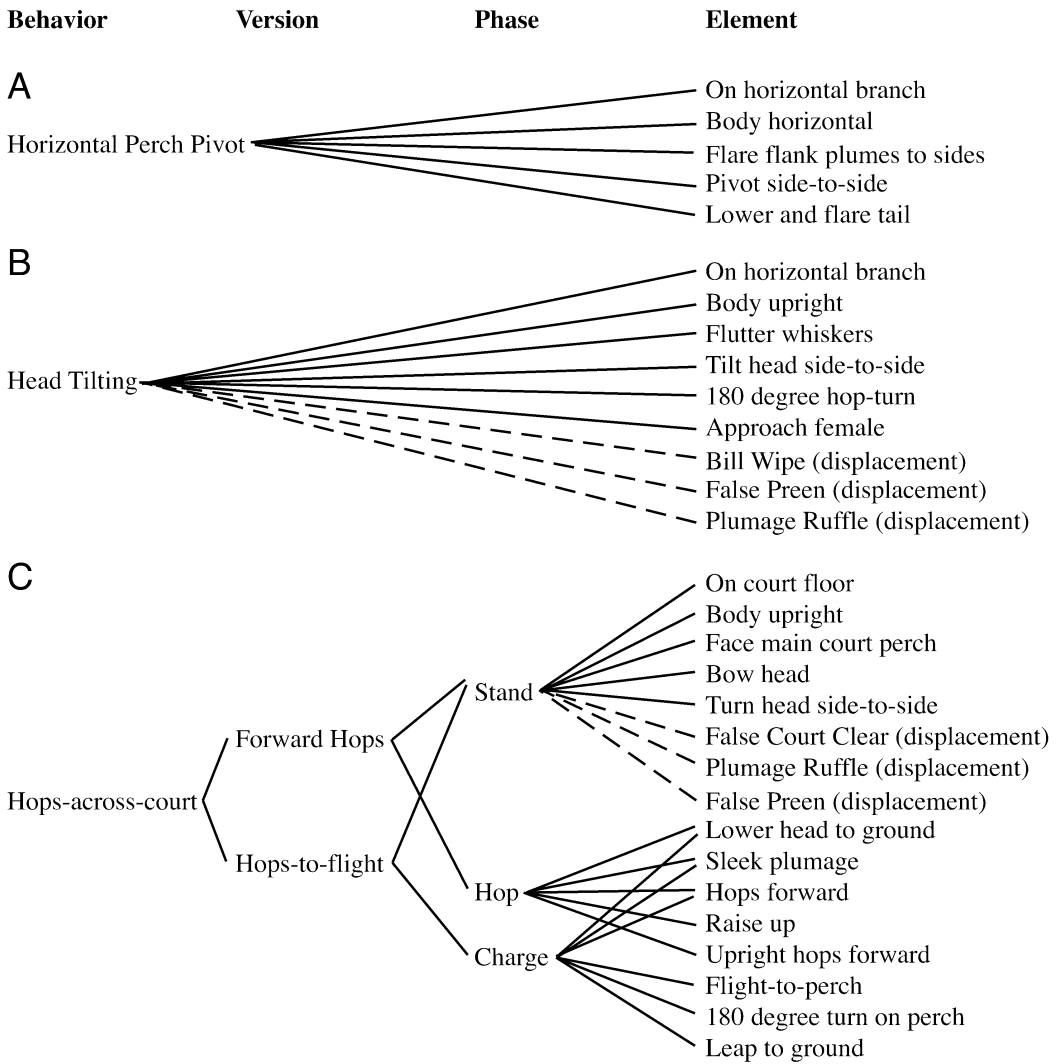


FIG. 5. Three schematic diagrams depicting the lower-level organizational structure for the male enticement displays. The "root" nodes on the far left under the subclass heading "Behavior" correspond to a terminal "tip" node of the same name in Figure 4. Dashed lines indicate components with some irregularity in the sequence.

Posture: body horizontal (or sloping with anterior lower than posterior); wings closed; flank plumes (Fig. 2 and Table 1) spread to form half-disc-shaped extensions on sides of body. Action patterns: pivoting leg joints to move torso left and right (about 90–110°); depressing, fanning, and shutting tail with each pivot. Spatial movement: slight lateral movement along perch (small steps, no hopping).

Head tilting.—An enticement display from early in the display sequence (Fig. 4). The head

is quizzically tilted left and right repeatedly to expose the underside of the throat to female-plumaged birds perched nearby on the main court perch (Fig. 11C, D). (Voucher clip: video no. 21682.) There are nine elements (Fig. 5B). Quantified components are summarized in Table 2. Place: horizontal perch adjacent to female-plumaged bird(s). Posture: body upright. Action patterns: tilting head side-to-side; fluttering throat whiskers (Fig. 2 and Table 1); 180° hop-turns. Spatial movement: moving along perch to

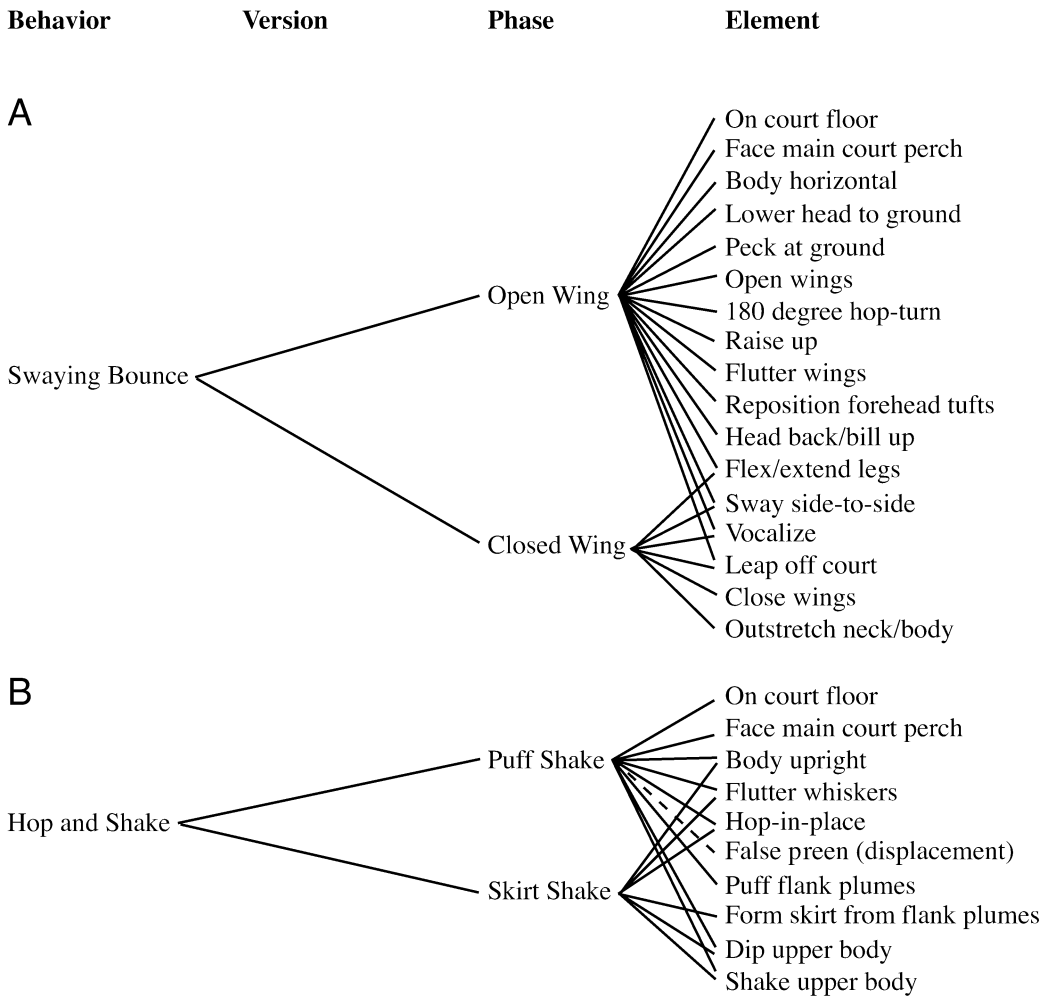


FIG. 6. Two schematic diagrams depicting the lower-level organizational structure of male precoition displays. The “root” nodes on the far left under the subclass heading “Behavior” correspond to a terminal “tip” node of the same name in Figure 4. Dashed lines indicate components with some irregularity in the sequence.

approach female. Other action patterns: leaf presentation; bill wipe; false preen; plumage ruffle.

Hops-across-court.—An enticement display (Fig. 4) comprising bounding hops, back and forth, from one end of the court floor to the other (Fig. 11E, F). (Voucher clips: video nos. 21682–21684.) There are 14 elements subdivided into three phases and two versions (Fig. 5C). Quantified components are summarized in Table 2. Place: court floor, facing main court perch. Posture: body upright; head bowed. Action patterns: turning head side-to-side; lowering head to ground; sleeking plumage; hopping forward;

raising up; hopping forward, upright; flying to perch; turning 180° on perch; leaping to ground. Spatial movement: moving across court in one direction; pausing at edge; returning to origin. Other action patterns: false court-clearing; ruffling plumage; false preening; leaf presentation.

Swaying bounce.—The first presentation display in the display sequence (Fig. 4). A long series of exaggerated, wobbling, up-and-down leg thrusts on the court floor, with wings open to the sides and fluttering in one phase, and tightly closed in another (Fig. 12A–H). (Voucher clips: video nos. 21685–21688.) There are 16 elements

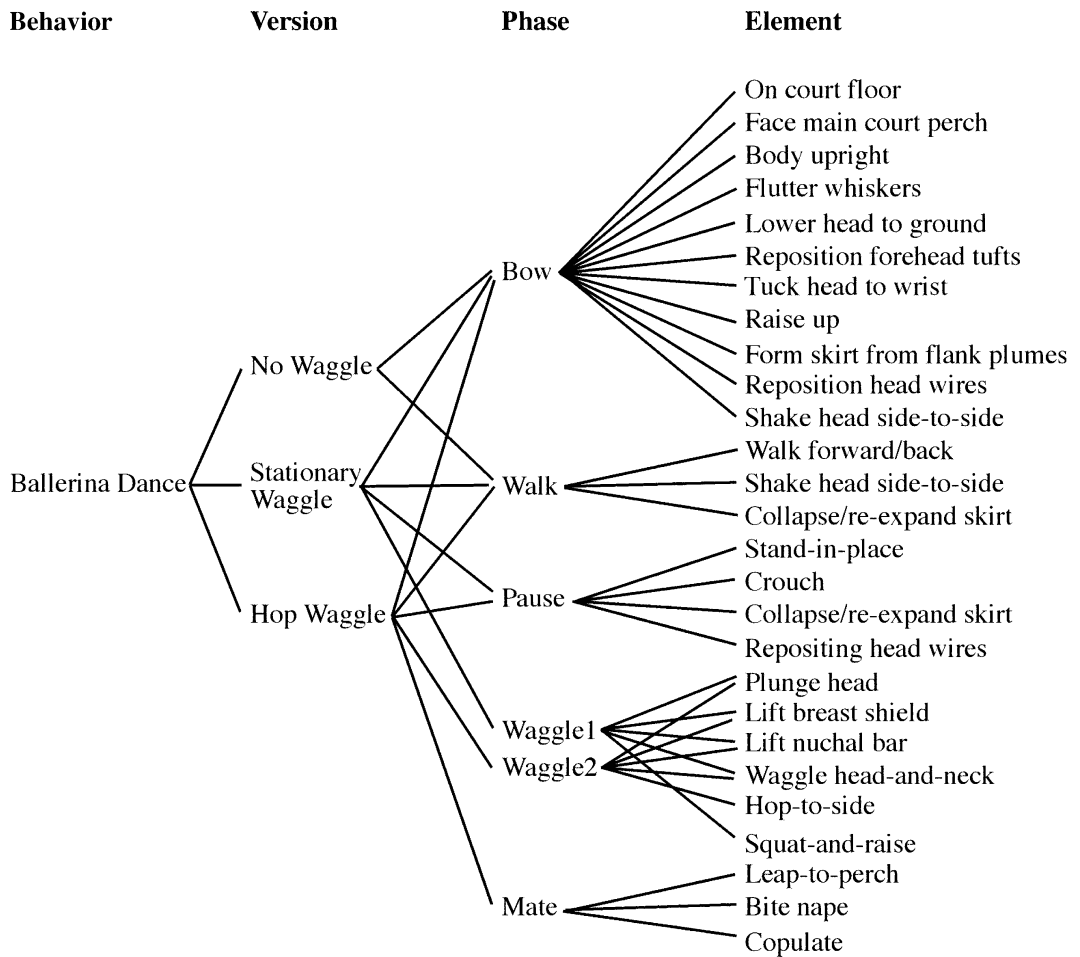


FIG. 7. A schematic diagram depicting the lower-level organizational structure for the ballerina dance display. The "root" node on the far left under the subclass heading "Behavior" corresponds to the terminal "tip" node of the same name in Figure 4.

subdivided into two phases (Fig. 6A). The second phase (closed-wing phase) was not observed at Mt. Stolle. Quantified components are summarized in Table 2. Note variation in degree of wing fluttering between populations (see voucher clips). Place: court floor facing main court perch. Posture: body horizontal; head near ground. Action patterns: pecking at ground; opening wings; 180° hop-turn; head back, bill up; repositioning forehead tufts (Fig. 2 and Table 1); fluttering wings; flexing and extending legs (squat and rise); swaying side-to-side; outstretching neck; closing wings; leaping off court; vocalizing. Spatial movement: stationary; the only movement is off-court, at the end of bouncing.

Hop-and-shake.—A presentation display (Fig. 4). Hopping in place with exaggerated ruffling and shaking of plumage (Fig. 13A–H). (Voucher clips: video nos. 21689–21692.) There are nine elements subdivided into two phases (Fig. 6B). Quantified components are summarized in Table 2. Note the major difference in tempo (shakes per second) between populations (see voucher clips). Place: court floor, facing main court perch. Posture: body upright. Action patterns: fluttering throat whiskers; hopping in place (flexing toes); ruffling flank plumes; lowering and raising upper body; shaking upper body; forming skirt. Spatial movement: largely stationary.

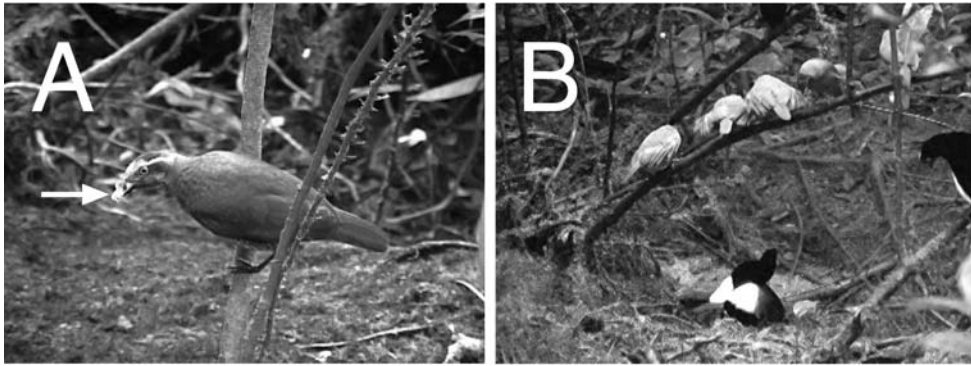


FIG. 8. Two female behaviors: (A) object gathering (video nos. 21669 and 21670), (B) display observation (video no. 21671) and wing shivering (video no. 21672).

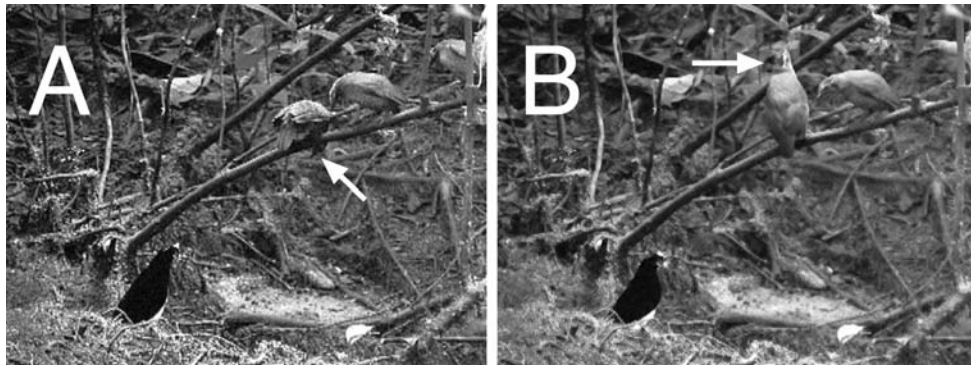


FIG. 9. An ethogram of upward bill-point sway display (video no. 21673): (A) the lowest point (arrow shows position of bill); (B) the highest point (arrow shows position of bill while “pecking at the air.”

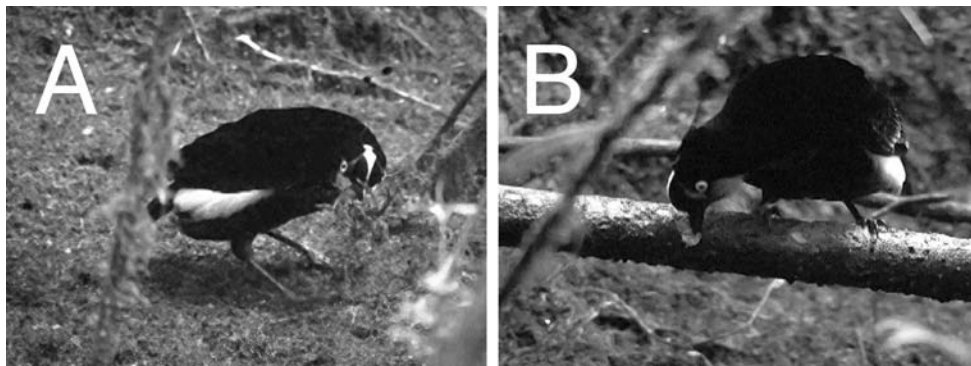


FIG. 10. Two male nondisplay behaviors: (A) mat construction (video no. 21675) and (B) object rubbing (video no. 21676).

TABLE 2. Summary of quantified aspects of male displays. Values are reported as the mean \pm SE where appropriate. An asterisk indicates a value calculated from a subsample of total observations.

Display	Mt. Stolle	Crater Mountain
Horizontal perch pivot		
Display frequency (displays h ⁻¹)	0.042	0.054
Number of bouts observed	4	5
Bout duration (s)	23.00 \pm 9.45	36.80 \pm 9.12
Pivot frequency (turns s ⁻¹)	0.90 \pm 0.12	0.79 \pm 0.13
Head tilting		
Display frequency (displays h ⁻¹)	0.042	0.087
Number of bouts observed	4	8
Bout duration (s)	59.50 \pm 27.00	31.36 \pm 5.51
Tilting frequency (tilts s ⁻¹)	0.41 \pm 0.08	0.40 \pm 0.03
Hops-across-court		
Display frequency (displays h ⁻¹)	0.074	0.109
Number of bouts observed	7	10
Lap duration (s)	7.36 \pm 1.55	9.31 \pm 1.48
Lap frequency (laps display ⁻¹)	4.00 \pm 0.65	2.30 \pm 0.26
Swaying bounce		
Display frequency (displays h ⁻¹)	0.063	0.217*
Number of bouts observed and quantified	6	20
Open-wing phase duration (s)	14.50 \pm 5.45	33.12 \pm 3.00
Bounce frequency (bobs s ⁻¹)	2.00 \pm 0.16	2.82 \pm 0.14
Closed-wing phase duration (s)	NA	57.00 \pm 25.77
Bounce frequency (bobs s ⁻¹)	NA	2.86 \pm 0.15
Hop-and-shake		
Display frequency (displays h ⁻¹)	0.305	0.326
Number of bouts observed	29	30
Puff shake frequency (shakes h ⁻¹)	0.38 \pm 0.03	0.54 \pm 0.04
Skirt shake frequency (shakes h ⁻¹)	0.35 \pm 0.02	0.30 \pm 0.02
Ballerina dance		
Display frequency (displays h ⁻¹)	0.368	0.434
Number of bouts observed	35	40
Bow phase duration (s)	1.78 \pm 0.04	1.96 \pm 0.05
Walk phase duration (s)	3.41 \pm 0.16	2.77 \pm 0.10
Pause phase duration (s)	5.15 \pm 0.35	6.39 \pm 0.37
Hops-to-side waggle version	15 of 35	28 of 40
Hop frequency (hops h ⁻¹)	0.76 \pm 0.05	1.08 \pm 0.06
Hops bout ⁻¹	4.47 \pm 0.19	8.82 \pm 0.87
Stationary waggle version	11 of 35	3 of 40
Waggle frequency (waggles h ⁻¹)	3.04 \pm 0.41	2.99 \pm 0.49
Waggles bout ⁻¹	39.30 \pm 13.29	13.33 \pm 7.42
Squat-and-raise frequency (no. h ⁻¹)	0.60 \pm 0.16	0.90 \pm 0.15
Squat-and-raise cycles bout ⁻¹	2.67 \pm 1.67	10.27 \pm 2.88
No-waggle version	6 of 35	4 of 40

Ballerina dance.—The quintessential high-intensity *Parotia* display. Flank plumes are positioned around the body in a manner resembling a ballerina's tutu as the bird performs an intricate dance (Figs. 14–17). (Voucher clips: video

nos. 21693–21696.) There are 23 elements, five phases, and three versions (Fig. 7). Quantified components are summarized in Table 2. Place: court floor, facing horizontal perch; on horizontal perch. Posture: body upright. Action

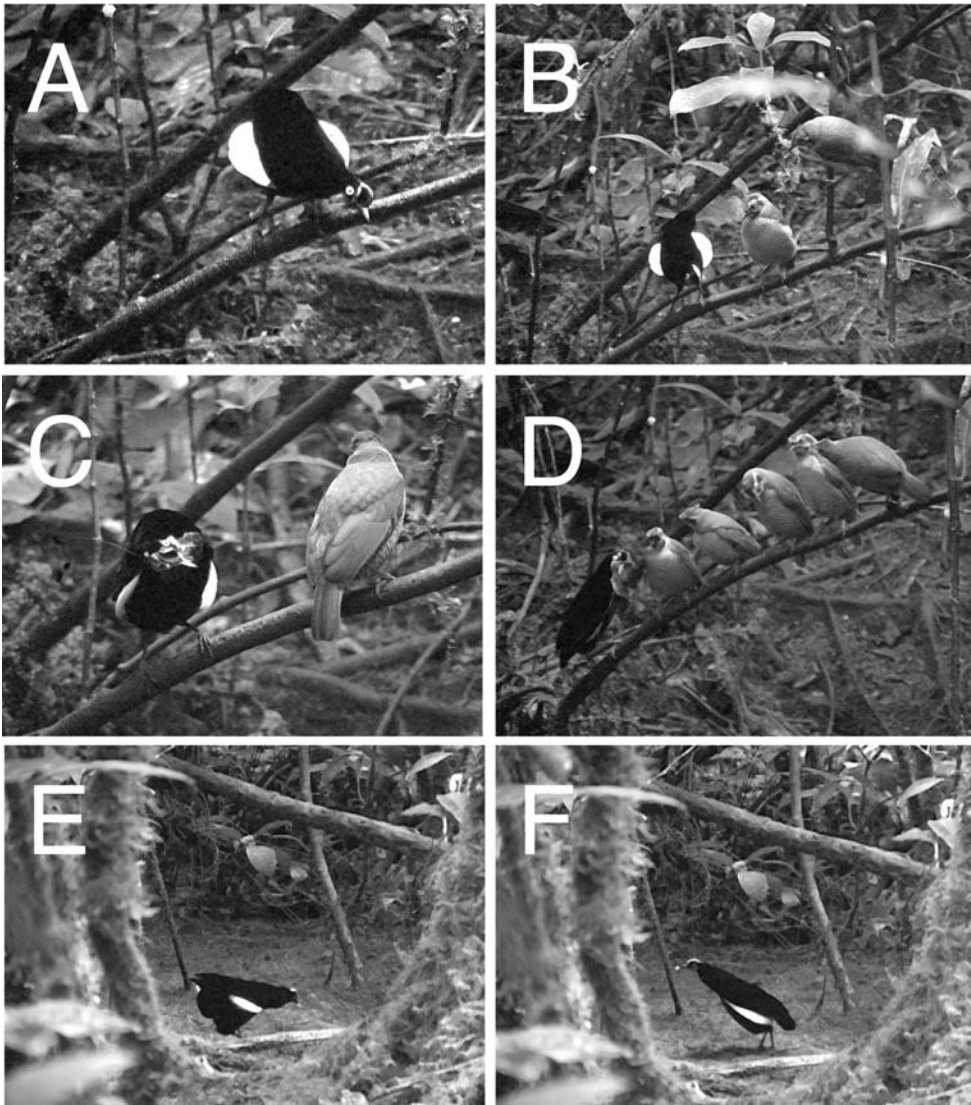


FIG. 11. Three male enticement displays: (A) horizontal perch pivot (video no. 21680) before arrival of a female on the court, (B) horizontal perch pivot to visiting females, (C and D) head-tilting (video no. 21681) to visiting female(s), (E and F) hops-across-court (video nos. 21682–21684), forward hops version, hop phase.

patterns: fluttering whiskers; lowering head to ground; repositioning forehead tufts (pushed forward over supranarial tufts); tucking head to wrist; raising up; forming skirt from flank plumes; repositioning head wires (in front of bill); shaking head side-to-side; walking forward and back; collapsing and expanding skirt; standing in place; crouching; repositioning head-wires (to sides of head); plunging head

into body; lifting breast shield (Table 1 and Fig. 2); lifting nuchal bar (Table 1 and Fig. 2); wagging head and neck; hopping to sides; flexing and extending legs (squat and rise); leaping to perch; biting nape; copulating. Spatial movement: forward and backward movement on court floor; lateral movement from hops-to-side; movement from court floor to main court perch (if copulation attempt).

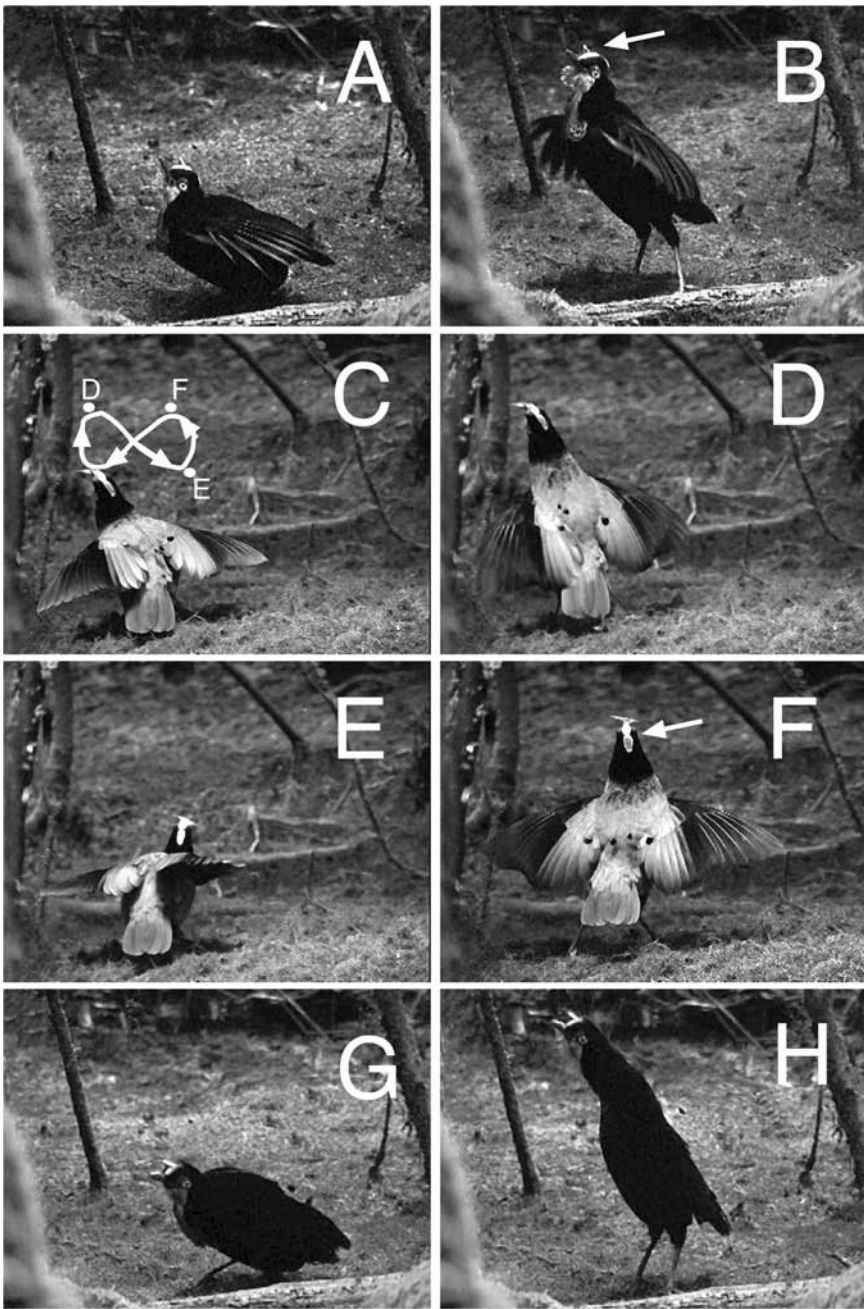


FIG. 12. An ethogram of swaying bounce display (video nos. 21685–21688): (A) low point of opening phase, (B) high point of open-wing phase (arrow shows position of frontal crest), (C–F) sub-adult male performing open-wing phase viewed from behind (diagram in box C shows trajectory of the head as seen from boxes D–F; arrow in box F shows position of frontal crest as seen from the perspective of a visiting female), (G) low point of closed-wing phase, and (H) high point of closed-wing phase.

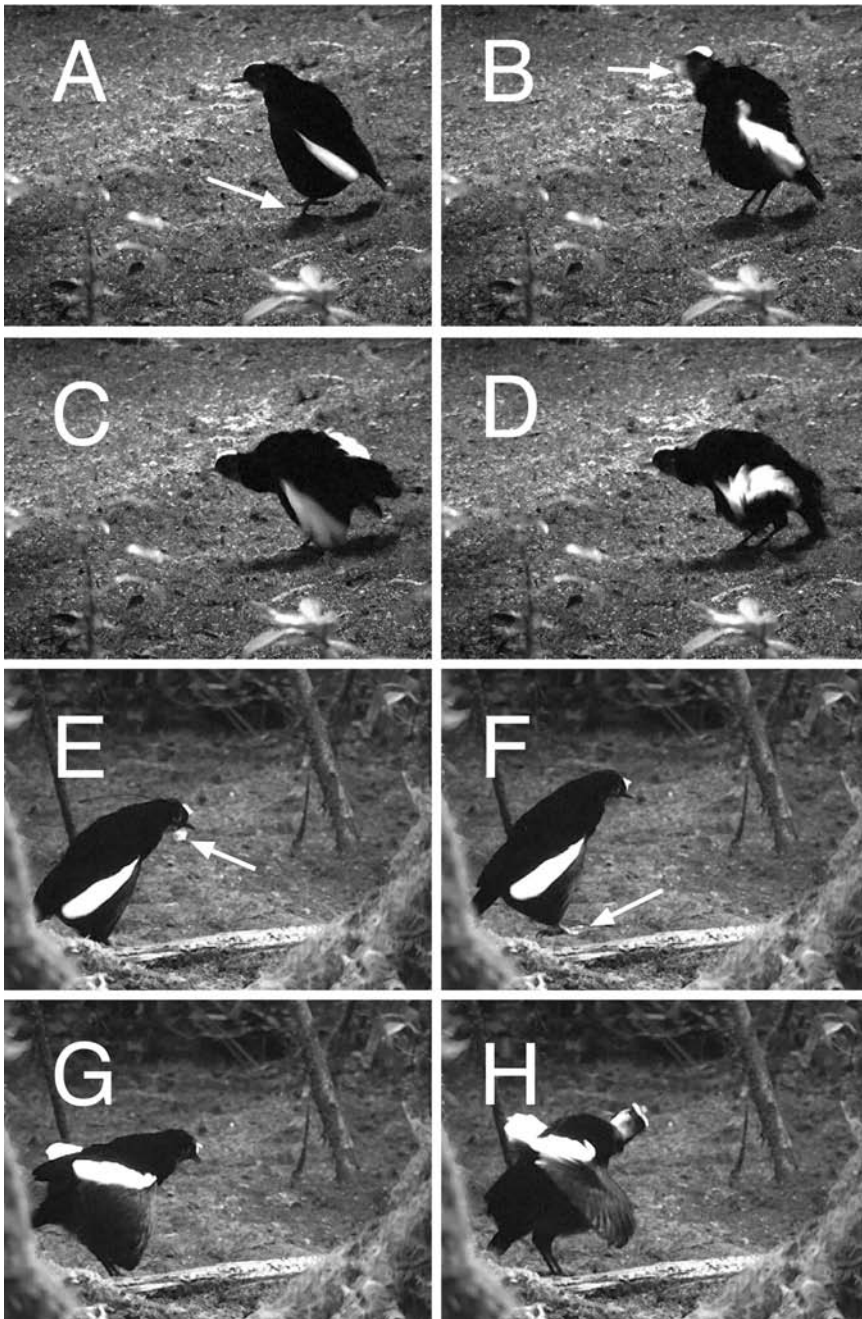


FIG. 13. An ethogram of hop-and-shake display (video nos. 21689–21692): (A–D) puff shake phase (arrow in box A highlights the hop-in-place element, and arrow in box B shows whisker fluttering), (E–H) skirt shake phase (arrow in box E shows whisker fluttering, and arrow in box F shows feet off ground).

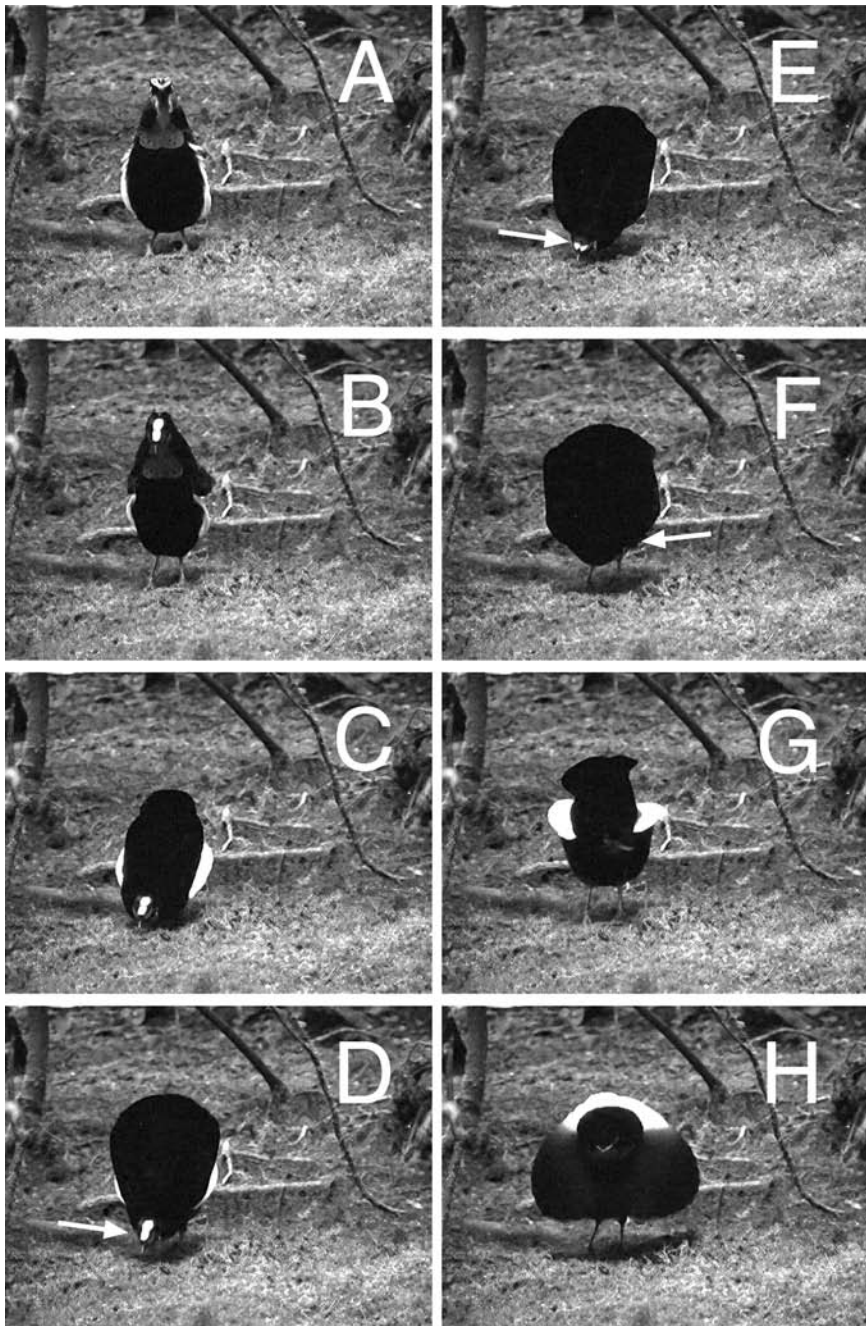


FIG. 14. An ethogram of bow phase of the ballerina dance display (both versions) (video nos. 21693–21696): (A) body upright and fluttering whiskers, (B and C) lowering head to ground, (D and E) repositioning forehead tufts (forward) (arrows highlight frontal crest), (F) tucking head (arrow points to position of right eye), (G and H) raising up, forming skirt from flank plumes, and repositioning head wires (forward).

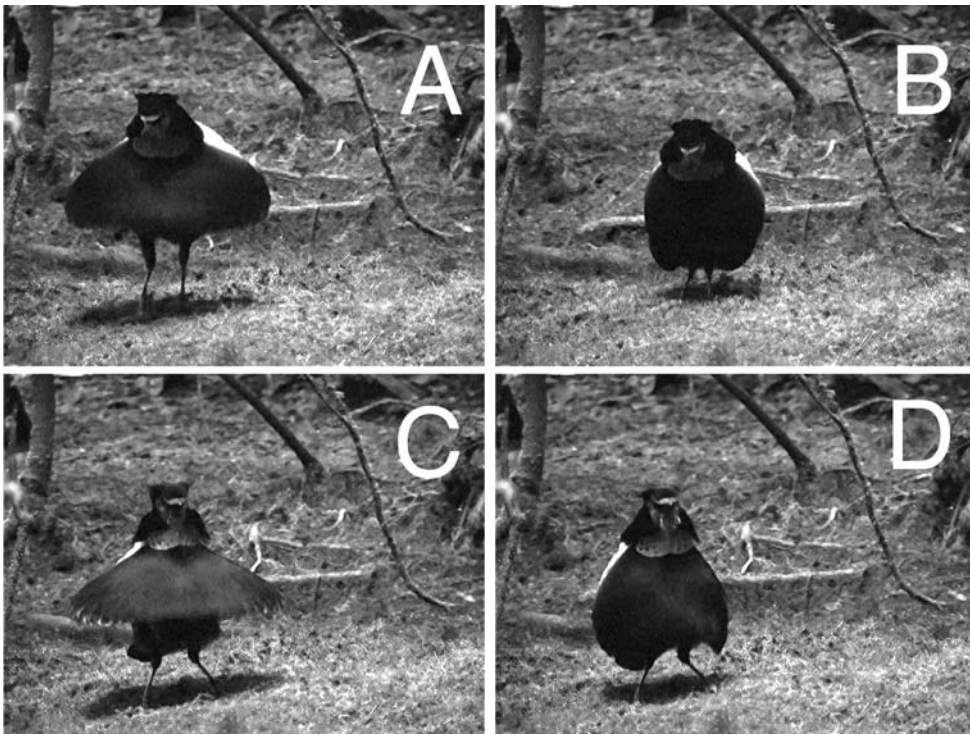


FIG. 15. An ethogram of head-shake-walk and stationary-pause phases of the ballerina dance display (both versions) (video nos. 21693–21696): (A and B) walking forward and back, shaking head, and collapsing and re-expanding skirt, (C and D) standing in place, crouching, collapsing and re-expanding skirt, and repositioning head wires (to sides).

The following data are not included in Table 2. Percentage of occurrence of each version at Mt. Stolle: 42.9% (15 of 35) hops-to-side waggle, 31.4% (11 of 35) stationary waggle, 17.1% (6 of 35) no waggle, and 8.6% (3 of 35) “mixed.” Percentage of occurrence of each version at Crater Mountain: 70% (28 of 40) hops-to-side waggle, 7.5% (3 of 40) stationary waggle, 10% (4 of 40) no waggle, and 12.5% (5 of 40) were “mixed.”

Leaf presentation.—An accessory display (Fig. 4). Any display performed with a small object, usually a white or yellow leaf held in the bill (Fig. 18A–C). Observed in conjunction with five displays: horizontal perch pivot, hops-across-court, head-tilting, swaying bounce, and hop-and-shake.

DISCUSSION

The most significant contribution of the present study is the relatively complete picture of courtship and mating behavior of Carola’s

Parotia that emerges from explicitly dissecting the “anatomy” of courtship. These results set a new standard for the descriptive ethology of birds of paradise and provide a strong foundation for studying the patterns and processes of evolutionary transformation of the extraordinary courtship-based phenotypes for which the family is renowned. The results also exemplify how modern ethological information can be formulated to facilitate incorporation into existing bioinformatics databases.

The courtship ethology of Carola’s Parotia is extremely complex—as complex as that of any bird of paradise, and therefore as that of any bird. The nature of this complexity is summarized in Figures 4–7, which depict the various levels of integration and hierarchical organization of the components that constitute the behavioral component of the phenotype. At the highest levels (Fig. 4), there are 20 behaviors partitioned among the sexes, two context-dependent categories, and a suite of

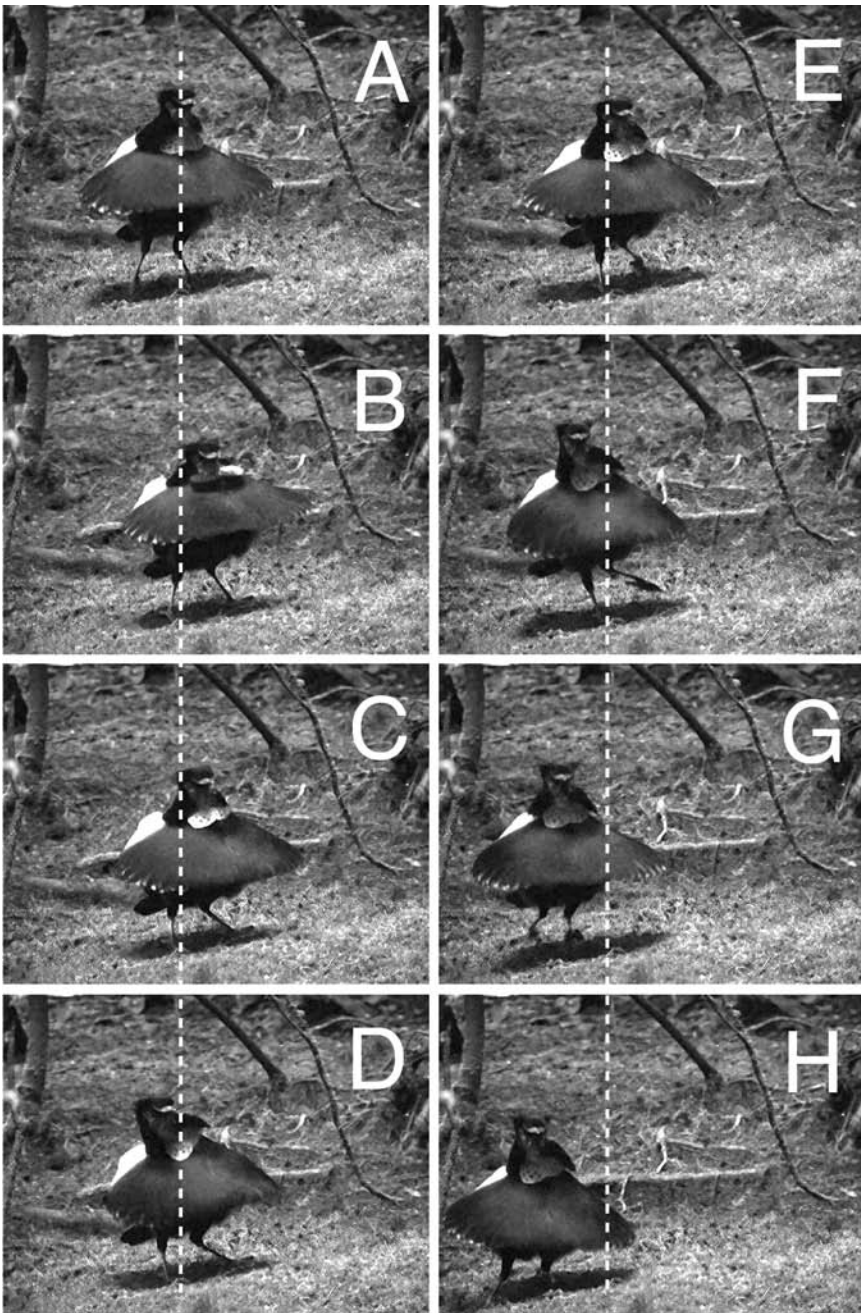


FIG. 16. An ethogram of head-and-neck waggle phase of the hop waggle version of the ballerina dance display (video no. 21695): (A–C) plunging head, lifting breast shield, and lifting nuchal bar, (D and E) wagging head, (F–H) hops-to-side. Dotted white line represents an imaginary line through the same place on the court through time to highlight the range of motion during the hops-to-side element.

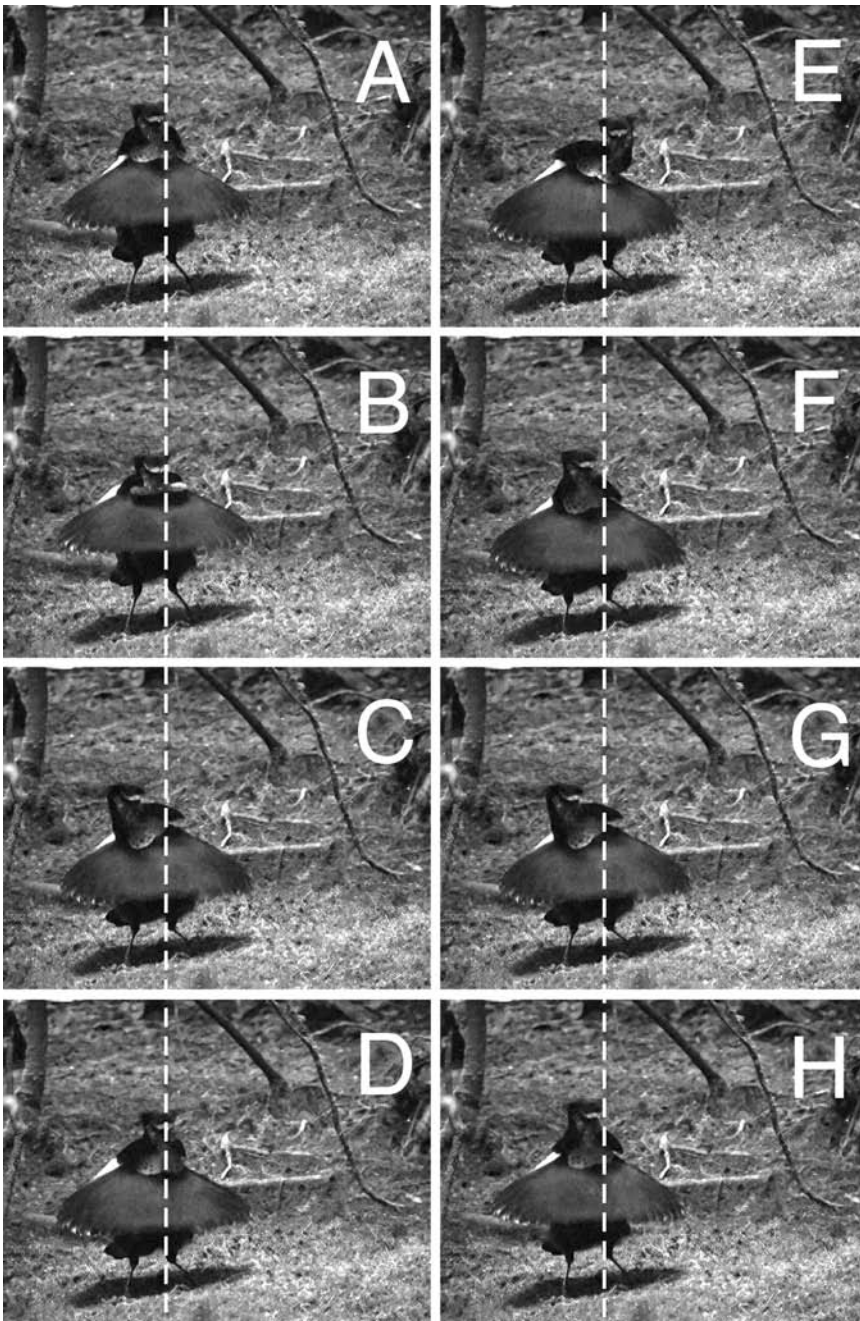


FIG. 17. An ethogram of head-and-neck waggle phase of the stationary waggle version of the ballerina dance display (video nos. 21693–21694): (A and B) plunging head, lifting breast shield, and lifting nuchal bar, (C–D) wagging head (to right), (E–H) wagging head (to left), squatting and rising. The dotted white line represents an imaginary line through the same place on the court through time to highlight the range of head and neck.

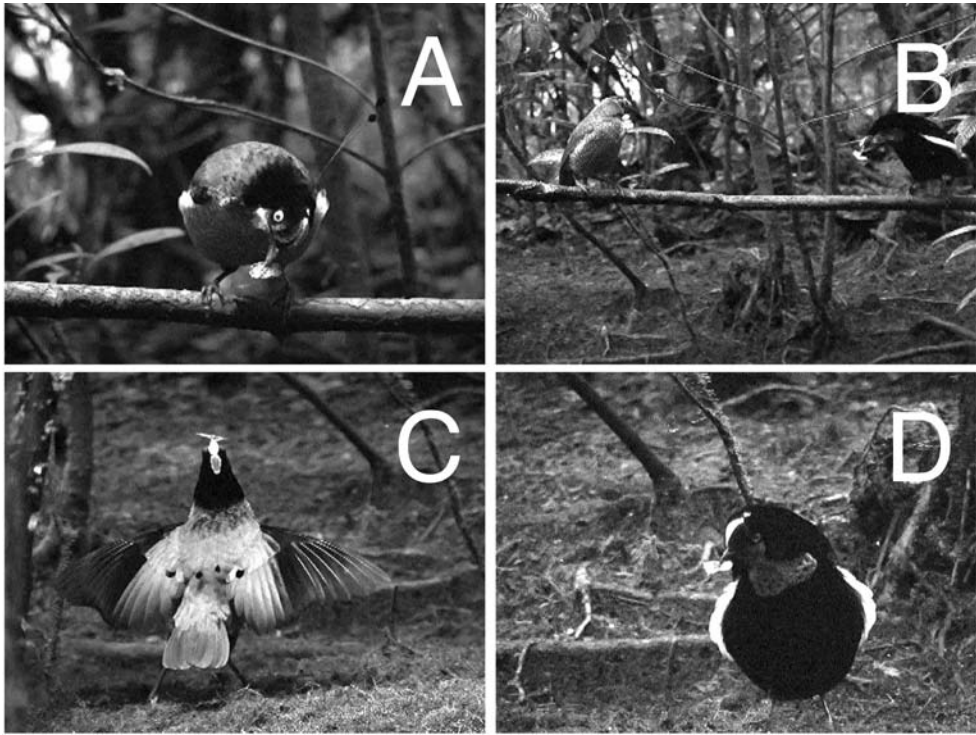


FIG. 18. Leaf presentation accessory display: (A) during the horizontal perch pivot display, (B) during the head-tilting display, (C) during the swaying bounce, and (D) during the hop-and-shake display).

functional categories. At the lower levels (Figs. 5–7), examined for male displays only, behavior patterns comprise many smaller units and subunits, including a total of 58 distinct elements. It is the structure of the many smaller units and subunits (i.e., versions, phases, and elements) that give rise to much of the overall complexity, and this structure (i.e., display anatomy) is the subject of the following discussion.

What is immediately apparent from examining the lower levels of integration and organization is that the phenotype is inherently modular (Figs. 5–7). Phenotypic modularity refers to discrete, hierarchically arranged units and subunits critical to the development and evolution of phenotypic complexity (Raff 1996, Wagner 1996). Modules are the building blocks of development within an organism, and they are the units of evolutionary transformation among species (Wagner 1996). Although rarely applied to ethology, modularity is nevertheless a fundamental concept, because modular units are believed to be the targets of selection and

the vehicles of diversification that create complexity at all levels (Wagner 1996).

The modular nature of Carola's Parotia courtship displays is evident in several forms: (1) the recurrent use, (2) differential employment, and (3) addition–deletion of various units and subunits that constitute the phenotype. Each form is discussed below.

Modularity is evident in the instances where units or subunits are used recurrently within the courtship phenotype. Although there are many examples, a particularly good example is the recurrence of displacement behavior patterns (e.g., bill wiping, plumage ruffling, etc.; Fig. 4). These behavior patterns recur throughout the courtship phenotype, both as independent entities and as subcomponents of larger, more complex units. Displacement behavior patterns are clearly incorporated as subcomponents of at least three displays: head-tilting (Fig. 5B), hops-across-court (Fig. 5C), and the hop-and-shake (Fig. 6B). In addition, there is evidence of the recurrence of units with much

less semi-independence (i.e., in units that never stand alone) than the displacement behaviors. For example, the element “flutter whiskers” is recurrent in three different displays: head-tilting (Fig. 5B), hop-and-shake (Fig. 6B), and the ballerina dance (Fig. 7).

Modularity is also evident from the observation that displays comprise numerous integrated subunits (i.e., the elements), and those subunits are variously employed into arrays that constitute additional entities or phases. Phases mark discrete temporal boundaries around the subsets of elements that make up otherwise continuous behavior patterns. For instance, a given rendition of the ballerina dance may terminate abruptly before being expressed to completion, but the abrupt end is always at a phase “break.” In other words, once a phase is initiated, it runs to completion even though the larger unit (i.e., the display) may not. Hence, although the ballerina dance is a discrete unit, it nevertheless comprises several integrated semi-autonomous subunits that have a smaller degree of sub-independence.

At a slightly higher level of integration, modularity is also apparent in the formation of versions. Alternative versions of the displays seem to be the result of differential addition and deletion of phases. For example, in the ballerina display (Fig. 7), each of the three versions comprises a different subset of the five phases. The simplest version, the no-waggle version, comprises only two phases (bow and walk), whereas the more complex versions, the hop waggle and stationary waggle, comprise five and four phases, respectively. This same pattern is also evident in the hops-across-court display (Fig. 5C).

Because versions are as highly integrated as the larger behavior patterns of which they are a part (i.e., the displays), they may represent the transitional stage in the formation of novel behavior patterns. For example, the emergence of additional independence in the components of the hops-to-flight version of the hops-across-court display (Fig. 5C) could easily allow for the origination of a “new” display—a “flight-charge” display that is expressed independently of the hops-across-court.

At an even higher level, the display behaviors themselves might be viewed as modular units within the entire courtship sequence (i.e., repertoire), so that among *Parotia* species, behaviors are rearranged, added, and deleted, creating

intertaxon complexity at the level of repertoires. Until enough other species are examined at a comparable level of detail for phylogenetic analysis, this possibility is only a reasonable hypothesis. The idea of intertaxon differentiation is consistent with the observed differences in behavior between the two populations. These differences point to a level of geographic complexity not explicitly evident in the hierarchical framework depicted here. These differences are evidence of the type of among-population changes that would be needed or expected in the origination of new taxa (subspecies or species). For instance, variation in vocalizations between the two study populations is greater than the variation among all the known vocalizations for all other species in the genus (Frith and Beehler 1998). The Mt. Stolle population has a three-note “*kwoi-kwoi-eeng*” and the Crater Mountain population has a single frantic “*kwa-a-a-ng*” note. Beyond vocalizations, several behavioral differences between the populations were observed. For example, the closed-wing phase of the swaying bounce display was not recorded at Mt. Stolle. If this major unit is absent from the courtship sequence, it could be an instance of differential gain or loss of an ethological module between the relatively recently isolated lineages. Another qualitative difference in the same display, the swaying bounce, is in the range of wing motion during the open-wing phase. This may indicate the origination of an additional unit or subunits, but further evidence is required. Also, there are quantitative differences in the tempo of the hop and shake display among the populations, the rate of shakes per second being faster at Crater Mountain (Table 2). Additional study should be done to examine more carefully these quantitative differences to determine whether they are consistent and significant.

Finally, although the use of video (or film) for collecting behavioral data is not new, this study shows that recent technological advances have nevertheless provided an opportunity for data collection and analysis on a scale that would have been impractical as recently as a decade ago. Availability of affordable, high-quality digital video cameras suitable for use in difficult field conditions, modern video-editing software, and the ability to stream video over the internet have changed the landscape of descriptive ethology. For the first time in the history of the discipline, ethological data can be vouchered and archived

for subsequent review and re-analysis in a way comparable to most other phenotypic data and genetic data. Etho-vouchers give an element of repeatability that is especially important for independent assessment of behavioral homology, which will greatly affect evolutionary ethology research. This transformation also stands to have a great effect on ornithology, because it opens the door for sophisticated studies of ethology in wild birds.

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LITERATURE CITED

- BARD, J. 2003. Ontologies: Formalising biological knowledge for bioinformatics. *BioEssays* 25:501–506.
- BARD, J. B. L., AND S. Y. RHEE. 2004. Ontologies in biology: Design, applications and future challenges. *Nature Reviews* 5:213–222.
- BOSTWICK, K. S., AND R. O. PRUM. 2003. High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *Journal of Experimental Biology* 206:3693–3706.
- CHARIF, R. A., C. W. CLARK, AND K. M. FRISTRUP. 2003. *Raven 1.0 User's Manual*. Cornell Laboratory of Ornithology, Ithaca, New York.
- COATES, B. J. 1990. *The Birds of Papua New Guinea*, vol. 2. Dove, Alderley, Australia.
- COOPER, W. T., AND J. M. FORSHAW. 1977. *The Birds of Paradise and Bower Birds*. Collins, Sydney, Australia.
- EIBL-EIBESFELDT, I. 1970. *Ethology: The Biology of Behavior*. Holt, Rinehart and Winston, New York.
- FRITH, C. B. 1968. Some displays of Queen Carola's Parotia. *Avicultural Magazine* 74: 85–90.
- FRITH, C. B., AND B. M. BEEHLER. 1998. *The Birds of Paradise: Paradisaeidae*. Oxford University Press, Oxford.
- FRITH, C. B., AND D. COLES. 1976. Additional notes on displays of Queen Carola's Bird of Paradise. *Avicultural Magazine* 82:52–53.
- FRITH, C. B., AND D. W. FRITH. 1981. Displays of Lawes's Parotia *Parotia lawesii* (Paradisaeidae), with reference to those of congeneric species and their evolution. *Emu* 81:227–238.
- GILLIARD, E. T. 1969. *Birds of Paradise and Bower Birds*. Natural History Press, Garden City, New York.
- GILLIARD, E. T., AND M. LECROY. 1961. Birds of the Victor Emmanuel and Hindenburg Mountains, New Guinea. *Bulletin of the American Museum of Natural History* 123: 1–86.
- HEALY, C. J. 1980. Display of Queen Carola's Parotia *Parotia carolae* (Paradisaeidae). *Papua New Guinea Bird Society Newsletter* 163–164:6–9.
- HUXLEY, J. S. 1966. Introduction: A discussion on ritualization of behaviour in animals and man. *Philosophical Transactions of the Royal Society of London, Series B* 251:249–271.
- JOHNSON, K. P. 2000. The evolution of courtship display repertoire size in the dabbling ducks (Anatini). *Journal of Evolutionary Biology* 13:634–644.
- KENNEDY, M., H. G. SPENCER, AND R. D. GRAY. 1996. Hop, step and gape: Do the social displays of the Pelecaniformes reflect phylogeny? *Animal Behaviour* 51:273–291.

- LORENZ, K. 1941. Vergleichende bewegungstudien an Anatiden. *Journal für Ornithologie* 89:194–294.
- LORENZ, K. 1966. Evolution of ritualization in the biological and cultural spheres. *Philosophical Transactions of the Royal Society of London, Series B* 251:273–284.
- PATERSON, A. M., G. P. WALLIS, AND R. D. GRAY. 1995. Penguins, petrels, and parsimony: Does cladistic analysis of behavior reflect seabird phylogeny? *Evolution* 49:974–989.
- PRUETT-JONES, S. G., AND M. A. PRUETT-JONES. 1990. Sexual selection through female choice in Lawes' Parotia, a lek-mating bird of paradise. *Evolution* 44:486–501.
- PRUM, R. O. 1990. Phylogenetic analysis of the evolution of display behavior in the Neotropical manakins (Aves: Pipridae). *Ethology* 84:202–231.
- RAFF, R. A. 1996. *The Shape of Life: Genes, Development, and the Evolution of Animal Form*. University of Chicago Press, Chicago, Illinois.
- SCHENKEL, R. 1956. Zur Deutung der Balzleistungen einiger Phasianiden und Tetraoniden. *Ornithologische Beobachter* 53:182–201.
- SCHODDE, R., AND J. L. MCKEAN. 1973. The species of the genus *Parotia* (Paradisaeidae) and their relationships. *Emu* 73:145–156.
- SLIKAS, B. 1998. Recognizing and testing homology of courtship displays in storks (Aves: Ciconiiformes: Ciconiidae). *Evolution* 52: 884–893.
- TINBERGEN, N. 1951. *The Study of Instinct*. Clarendon Press, Oxford.
- TINBERGEN, N. 1959. Comparative studies of the behaviour of gulls (Laridae): A progress report. *Behaviour* 15:1–70.
- VAN TETS, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. *Ornithological Monographs*, no. 2.
- WAGNER, G. P. 1996. Homologues, natural kinds and the evolution of modularity. *American Zoologist* 36:36–43.

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