

Courtship ethology of Wahnes' parotia *Parotia wahnesi* (Aves: Paradisaeidae)

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Abstract The concept of modularity has not been fully incorporated into current thinking about the evolution of behavioral complexity. One limiting factor is the paucity of high-quality descriptive data exemplifying the organizational structure of complex behavioral phenotypes in which modular units are likely to exist. In this paper, I describe the courtship ethology of Wahnes' parotia, *Parotia wahnesi*, a little known bird of paradise endemic to northeastern Papua New Guinea. This paper builds upon existing and ongoing work on the genus *Parotia* by describing courtship a way that clearly and comprehensively illustrates ethological structure. Results reveal eleven diagnosable behavior patterns arranged within a seven-level hierarchical structure. Behavior comprises numerous discrete, semi-autonomous, hierarchically arranged units used to form additional units at higher levels of integration. Of the eleven behavior patterns, the three male displays are the most complex. Surprisingly, these displays comprise a similar number of elements as the displays of *P. carolae*, a species with twice the number of displays in its repertoire. These findings and others support the conclusion that the *P. wahnesi* courtship phenotype is inherently modular in organizational structure. Finally, this study emphasizes the importance of comprehensive descriptive studies to

increasing our understanding of the importance of biological principles, for example modularity, across a wider range of animal biodiversity.

Keywords Ethogram · Modularity · Ontology · Phenotypic complexity · Bird of paradise

Introduction

To understand the phylogenetic underpinnings of behavior, early ethologists emphasized the transformational origins of behavior—i.e. the pre-existing behavior patterns from which novelties are derived (Tinbergen 1951, 1952; Lorenz 1966; Eibl-Eibesfeldt 1970). This work grew from the view in which behavioral sequences, and their underlying sub-units, are regarded as similar to the rest of the phenotype in terms of inherent organizational properties and underlying mechanisms of evolutionary change (Lorenz 1950; Tinbergen 1950, 1952; Thorpe 1951; Hind 1953; Nelson 1973; Barlow 1977). Despite early emphasis, this “structural” approach to animal behavior has been less prominent than other areas of phenotypic biology. In morphology for instance, studies have shown that novel traits arise from ancestral phenotypes as a result of the evolutionary potential afforded by the modular nature of organismal design (Raff 1996; West-Eberhard 2003; Schlosser and Wagner 2004). In this view, novelties not only emerge as a product of selection acting on small-scale phenotypic mutations, but also via the reorganization of ancestral phenotypes during development (West-Eberhard 2003). This is possible because organisms are composed of numerous modular entities: discrete,

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semi-autonomous, hierarchically arranged units, and sub-units that are the building-blocks of development and evolution (Raff 1996; West-Eberhard 2003; Schlosser and Wagner 2004). Modularity has gained widespread acceptance among those who study large-scale morphological evolution but has yet to be incorporated into a general framework of ethological evolution. To help unify the study of animal phenotypes ethologists increasingly need to look for evidence of modular design in behavioral phenotypes across a large portion of animal biodiversity.

Identifying the modular units of behavior, however, requires high-quality descriptive data revealing the organizational structure of complex behavioral phenotypes (i.e. behavioral “anatomies”). Despite this, studies revealing ethological structure in a comprehensive format are relatively uncommon. One problem is that relative to other aspects of phenotype, behavior is difficult to characterize in a way that accurately depicts structural organization (Wenzel 1992). The fundamental components are, furthermore, often entirely unknown a priori (making straightforward description difficult) and behavioral form cannot be assessed from museum specimens. As a result, much behavioral data comes as abbreviated descriptions included within larger studies and not intended to give a complete picture of phenotypic organization.

A recent study of courtship ethology in Carola’s parotia, *Parotia carolae*, illustrates the importance of depicting the organizational structure of a complex behavioral phenotype (Scholes 2006). As a systematically compiled representation of the components comprising courtship and mating, this study gives a comprehensive overview of a complex ethological phenotype and uncovered preliminary evidence for the modular organizational structure of courtship in this species (Scholes 2006).

The objectives of this paper are both to build upon the existing groundwork and facilitate future comparative work (Scholes in preparation) by examining courtship ethology in Wahnes’ parotia, *P. wahnesi*. Specifically, my purpose was to discover, and describe for the first time, the components that comprise the organizational structure of *P. wahnesi* the courtship phenotype. In combination with other studies of similar scope and scale (Scholes 2006; Scholes in preparation) progress can be made toward addressing bigger issues such as the role of modularity in *Parotia* evolution.

Parotia wahnesi is a little known and geographically restricted bird of paradise found only in the mountains of the Huon Peninsula and isolated Adelbert Range of northeastern New Guinea (Frith and Beehler 1998). In

the Huon, the primary home of the species, it is known only in a narrow band of forest between 1,100 and 1,700 m elevation (Frith and Beehler 1998). In the Adelbert Mountains, *P. wahnesi* was unknown until 1974 (Pratt 1982) and has not been recorded there subsequently. Among the *Parotia*, *P. wahnesi* is unique, because of its long wedge-shaped tail, prominent bronze colored “pom-pom”-like frontal crest, and status as one of only five birds of paradise listed as “vulnerable” by the IUCN Species Survival Commission (Frith and Beehler 1998). Although its phylogenetic position is unknown, it has been hypothesized to be the most “primitive” *Parotia*, because of its long tail, which was thought to be a characteristic of arboreal displaying species, and therefore intermediate between a long-tailed, arboreal-displaying ancestor and the more derived short-tailed, ground-displaying species (Gilliard 1969). This hypothesis, although currently unsupported, nevertheless implicitly assumes the species is the least derived of the group and may, therefore, have the simplest courtship.

Current knowledge about the courtship of *P. wahnesi* is incomplete (Frith and Beehler 1998). Most data come from one captive male in the New York Zoological Park (now the Bronx Zoo) in 1939 (Crandall 1940) and a few observations of a captive from the Baiyer River Sanctuary in Papua New Guinea (PNG) (Coates 1990). Knowledge about display behavior in the wild comes from a few sightings of terrestrial display courts (Schodde and McKean 1973; Schodde and Mason 1974) and several isolated observations of display-like behavior away from the court (Frith and Beehler 1998). Nothing is known about the importance of specific displays for this species, but a study of Lawes’ parotia, *P. lawesii*, has revealed that mating success varies substantially among males and sexual selection operates via female choice (Pruett-Jones and Pruett-Jones 1990). Presumably there is variation among males in the performance of some display components and thus delineation of those components is critical for understanding function and pathways of evolution.

The approach used here to depict courtship ethology involves a multi-stage process of pattern recognition and identification of units, then anatomization of those units into their constituent parts—e.g. basal action patterns (elements), temporal stages (phases), and alternative forms (versions) at low levels, and classes for functional category, context, and gender specificity at higher levels. Data are presented as simplified text descriptions, photographic ethograms, schematic diagrams emphasizing the relational organization of components, and archived video with Internet-accessible vouchers for preservation, reference, and re-evaluation.

Study area

The courtship ethology of the *P. wahnesi* was studied in the wild in PNG (Fig. 1). The study area was in the Finnestere Mountains of the Huon Peninsula. This site was a remote field camp at ~1,850 m on southern watershed of the Finnestere Mountains, ~16.3 km south of the Teptep airstrip (06°6.034'S, 146°33.526'E). Fieldwork took place September 28–October 30, 2001.

Materials and methods

Local field assistants were employed to search the forest to find terrestrial display territories of adult males and to build observation hides. From hides, video recording of unmarked birds took place from 05:30 to 10:30 and again from 13:30 to 17:30. Video recording was done with a Sony DCR-VX2000 mini DV digital video recorder using both interlaced and non-interlaced recording formats. All video footage was imbedded with a date and time stamp. A total of 104 h of observation resulted in ~500 min of video for analysis.

Analysis of the major components of courtship ethology began with a five-stage process. In the first stage unedited video was imported from tape into a Macintosh computer and stored on a hard-drive using iMovie3 software from Apple Computers. Raw footage was then carefully reviewed so that major components could be identified. Once identified, each example of the major components were extracted and subdivided into individual clips that could be labeled, sorted, and analyzed independently. Individual clips representing the major components 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

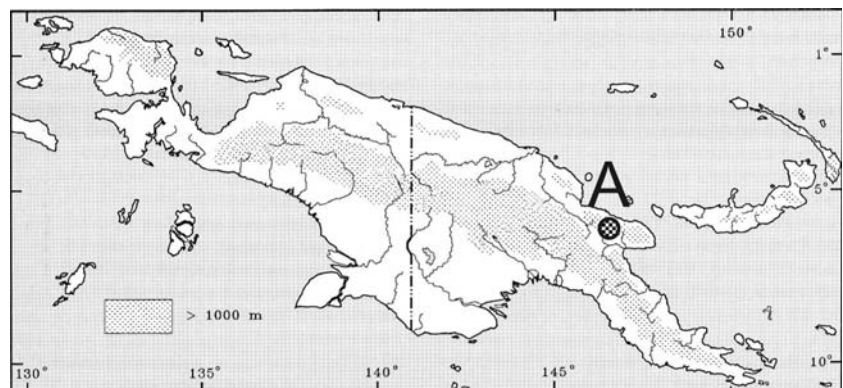
video and imported into Raven 1.0 (Charif et al. 2003) for analysis.

To examine the relational structure of the behavioral components comprising the *P. wahnesi* courtship phenotype a simple ontology was constructed and visualized with a series of schematic diagrams. Ontologies are formal conceptualizations in which entities are described both by their meanings and relationships to each other (Bard and Rhee 2004). The purpose of the diagrams is to depict the units described in the study and their interrelationships at different levels of integration. This format serves the important role of organizing a complex knowledge structure in a way that can be mined for content, modified, and updated more efficiently than traditional free-text descriptions alone.

The ontology has seven classes: three higher-level classes (sex, context, and function) depicting organization of the named behavior components (also a class) and three lower-level classes (versions, phases, and elements) showing organization of behavioral sub-units for male displays. The meaning of the two highest-level classes (sex and context) is unambiguous; the meaning of the third class, function, needs clarification, however. Functions as used here are putative hypotheses meant to aid understanding of phenotype organization and should be regarded as tentative assessments pending further study. Function terms are consistent with traditional or vernacular usage. For example, displacement refers to behavior components used out of typical context and enticement refers to behavior components used to attract females to a display area. Likewise, presentation refers to behavior components directed to a receiver (usually females) engaged in observation.

Text descriptions consist of an initial summary followed by a more detailed description of the place, posture, primary action patterns, spatial movement, and “other” action patterns. *Place* describes where the primary action pattern occurs (e.g. horizontal perch or

Fig. 1 Map of New Guinea with study area in the Huon Peninsula indicated with the hatched circle (A)



court floor). *Posture* is a description of general body orientation and a list of the relative positions of head, wings, legs, tail, and ornaments. *Action Patterns* is a description of primary body, appendage, and ornament motions. *Spatial Movement* describes changes in location during the behavior (e.g. lateral movement along perch). *Other Action Patterns* lists any other action patterns that are a part of the behavior but that have been described as independent units elsewhere (e.g. displacement behavior or vocalization). If one of these five sections is not relevant to a specific behavior, it is omitted.

Sequences depicting behavioral changes over time are illustrated with photographic ethograms derived from video frame-captures. Representative video clips are selected and digital images of individual frames are exported and edited to a subset depicting the range of motion. To improve visual clarity, images were processed with Photoshop (Adobe, San Jose, CA, USA) to balance color, correct brightness/contrast, and to remove compression/video artifacts (e.g. the de-interlacing tool). No additional alterations were made. The images were then arranged in temporal sequence with annotations (e.g. arrows, point-of-reference lines, etc.) added.

Videos used in the analysis, including voucher clips, are video specimens in the collections of Macaulay Library at the Cornell Laboratory of Ornithology, Ithaca, NY, USA. This collection is a permanent archive of biological specimens similar in aims and scope to “traditional” museum collections and digital collections, for example GenBank, but for ethological data. The purpose of the video vouchers is to provide unaltered (“raw”) material for reference and to facilitate further study. The entire video dataset used in the analysis has been accessioned with individual clips used as reference vouchers freely available online. Vouchers can be found at: <http://www.animalbehaviorarchive.org>. All voucher video clips have Macaulay Library sound and video catalog numbers (video_45950 through video_45970). Individual video vouchers can be located by searching the archive for a specific catalog number, or the entire set can be returned through an “advanced search” for the complete range of catalog numbers.

Results

External morphology

The external morphology of the courtship phenotype includes specialized ornaments unique to the genus

Parotia. Terminology for ornamental morphology used here is the same as described and illustrated in a previous study (Scholes 2006). Brief descriptions of important features of male ornamental plumage are provided to facilitate interpretation of behavior patterns (Table 1). The most distinctive plumage features of *P. wahnesei* relative to congeners are the long tail and the shape, size, and color of the frontal crest.

Display courts and leks

The courtship phenotype includes the architecture of display courts built and maintained by adult males (Schodde and Mason 1974; Frith and Beehler 1998). Courts examined are on relatively flat parts of gently sloping hillsides or wide, plateau-like, ridge tops ($n = 7$). Courts are irregular in shape; they range from approximately ~ 1.0 to ~ 3.0 m² ($n = 7$). Courts are typically placed beneath a dense thicket of shrubby undergrowth. The floor is cleared of leaf litter and vegetation so the substrate is roots and soil. All courts have at least one horizontal perch, herein called the main court perch, over the central part of the court. Main court perches range from ~ 0.5 m to more than 1 m above the court floor and range in diameter from approximately 2 to 10 cm. Court perches are used by males for some displays and by females when observing displays. Leaves are pruned from overhanging vegetation, but the extent of pruning is not as extensive as for other *Parotia* (Scholes, personal observation).

Lek structure is dispersed: courts appear solitary but are within auditory range of one another. Because all courts within the study leks were not located, nearest-neighbor distances were not calculated. Because of the

Table 1 Several important terms for characterizing ornamental plumage

Terms	Definitions
Head wires	Three wire-like feathers with spatulate tips that emanate from behind each eye; called “occipital plumes” Frith and Beehler (1998)
Nuchal bar	A narrow horizontal bar of highly iridescent blue-green feathers on the rear crown
Frontal crest	A complex arrangement of feathers on the forehead. Composed of three distinct parts: supra-narial tufts, forehead tufts, and loreal tufts. Called “forehead tufts” by Gilliard (1969) and “frontal feathering” by Shodde and McKean (1973)
Breast shield	A patch of large iridescent feathers on the upper breast
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

great distances between some courts (greater than 1 km), it seems likely the study area encompassed more than one lek.

Acoustic components

Parotia wahnesi courtship ethology includes several acoustic components. Male advertisement calls were frequently heard during observation session and 26 recordings were suitable for analysis. The most common call (13/26) is a harsh raspy two-note “yeah-yeah” or “yack-yack.” The other calls are similar, and differ only in the number of “yeah” notes included. Single-note and four-note calls were relatively uncommon (both 3/26) and three-note versions were the second most common (7/26). The “yeah” notes of all calls are very similar in acoustic structure; they average 0.280 ± 0.012 s in duration with most energy concentrated at 3.52 ± 2.56 kHz ($n = 12$). They are usually unstructured white-noise sounds with no pure tones or visible harmonics (Fig. 2A). Occasionally, however, some notes have a small amount of harmonic structure (first note in Fig. 2A).

In addition to advertisement calls, males emit a diversity of softer sounds around display courts. These sounds were variable and infrequent and so were not often recorded. Of those recorded, four types could be identified: a pure-tonal squeak (Fig. 2B), an ascending “weeet” (Fig. 2C), a slightly descending whine (Fig. 2D) and a raspy rolling trill-like “yaaat” (Fig. 2E).

In addition to vocal sounds, a conspicuous dove-like wing-whistle sonation (sensu Bostwick and Prum 2003) can be heard as the birds fly back and forth above a court on approach. A similar, but more tick-like, sonation is produced when the wings are flicked during the horizontal perch pivot display (see below).

Female courtship and mating behavior

Figure 3 summarizes the higher-level organizational structure. Lower-level organizational structure is not described for female behavior.

Court visitation (video_45950)

A female non-display mate-searching behavior (Fig. 3). It involves a range of activity in which visiting females move among perches to inspect the court area.

Display observation (Fig. 4A; video_45951)

A female non-display mate-sampling behavior (Fig. 3). While a male displays below, the female looks on from

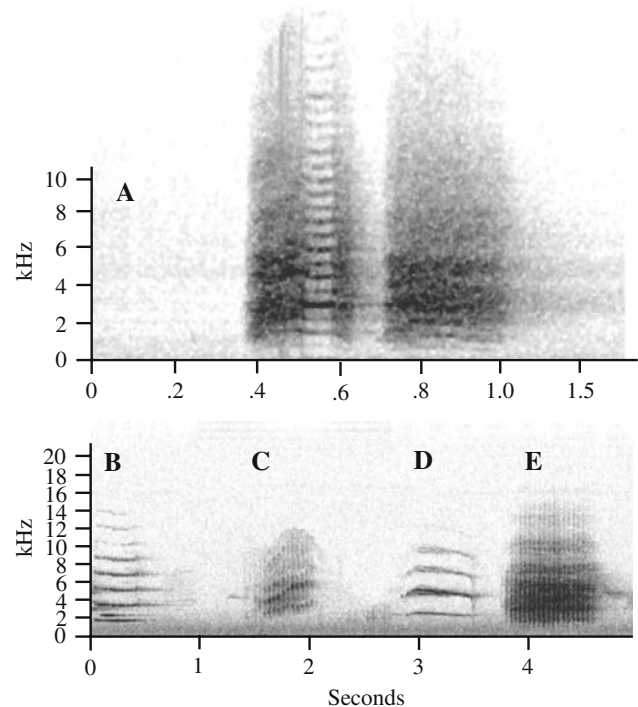


Fig. 2 Sonogram of common vocalizations: *A* two-note “yeah-yeah,” *B* pure-tone squeak, *C* ascending “weeet,” *D* descending whine, and *E* raspy trill-like “yaaat”

the main court perch and closely follows the movements of the male. *Place*—horizontal perch. *Posture*—body upright, horizontal, and sloping (head down/tail sloping upward behind body) (Fig. 4A). *Action Patterns*—180° hop-turns, flick wings open/shut, flick tail up and flair open/shut, lower head to perch (peer underneath perch; Fig. 4A), tilt head side-to-side, erect feathers behind eyes and back of head (Fig. 4A), ruffle plumage. *Spatial Movement*—lateral movement along perch, hops between adjacent perches.

Wing fluttering (Fig. 4B; video_45952 and 45953)

A female solicitation display (Fig. 3). While observing male display from the main court perch, the wings are opened slightly and twitched slowly. *Place*—horizontal perch above or adjacent to a displaying male (Fig. 4B). *Posture*—body horizontal to upright, wings partially open (Fig. 4B). *Action Patterns*—wings twitched (primaries expanded and shut), feathers behind eyes and back of head slightly erected.

Fig. 3 Schematic diagram depicting the higher-level relational structure for the eleven courtship and mating behavior components described in this study

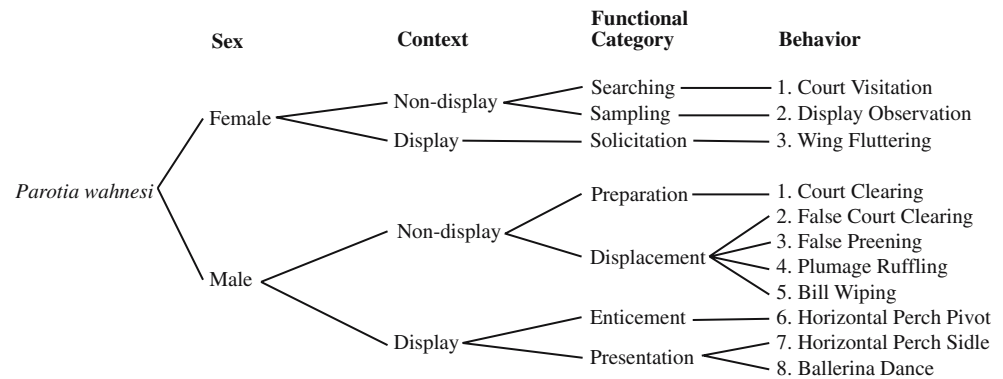


Fig. 4 Two female behavior components: **A** display observation (video_45951) and **B** Wing fluttering (video_45952 and 45953)

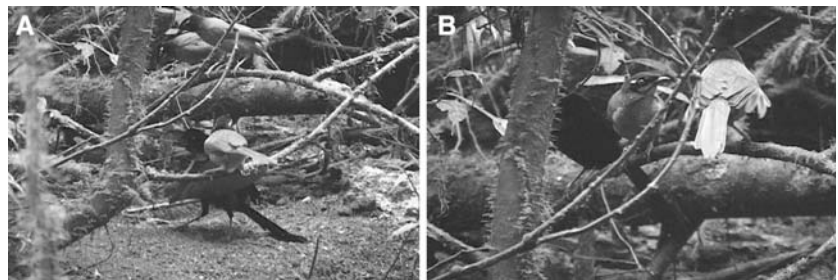


Fig. 5 Two male non-display behavior components: **A** court clearing (video_45960) and **B** plumage ruffling (video_45969 and 45970). The arrow in plate A points to a large leaf held in the bill and about to be tossed from the court



Male courtship and mating behavior

Higher-level organizational structure is summarized in Fig. 3 above. The lower-level organizational structure if display is described below.

Court clearing (Fig. 5A; video_45960)

A male non-display court preparation behavior (Fig. 3). A range of activity in which leaves, leaf litter, or other forest debris are removed from the court floor (Fig. 5A).

False court clearing (video_45961 and 45962)

A male displacement behavior (Fig. 3). Similar in form to court clearing. The head is suddenly 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.

False preening (video_45963)

A male displacement behavior (Fig. 3). A preen-like behavior in which the male seems to be pecking at feathers along the breast, flanks, and under the wing but the bill does not touch the feathers.

Plumage ruffling (Fig. 5B; video_45969 and 45970)

A male displacement behavior (Fig. 3). 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 (Fig. 5B).

Bill wiping (video_45959)

A male displacement behavior (Fig. 3). 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.

Horizontal perch pivot (Figs. 6A, B; video_45964 and 45965)

An enticement display (Fig. 3). Turns or rotations, from side-to-side (i.e. left and right) on a horizontal perch with tail cocked above the back and wings

flicked to the sides with each turn (Figs. 6A, B). It comprises ten elements (i.e. basal action patterns) (Fig. 7A). Quantified components are summarized in Table 2. *Place*—horizontal perch. *Posture*—body horizontal (Fig. 6A), head up, wings closed, tail lifted above back (Figs. 6A, B). *Action Patterns*—pivot torso left and right (Figs. 6A, B), flick wings open/shut with each pivot, fan/shut tail with each pivot, 180° hop-turns, downward “pointing” (bill pointed to ground, tail in line behind body), leap from perch (to ground or off court). *Spatial Movement*—lateral movement along perch. *Other Action Patterns*—Bill wiping.

Fig. 6 Range of motion in the horizontal perch pivot (video_45964 and 45965): **A** pivot to the right and **B** pivot to the left

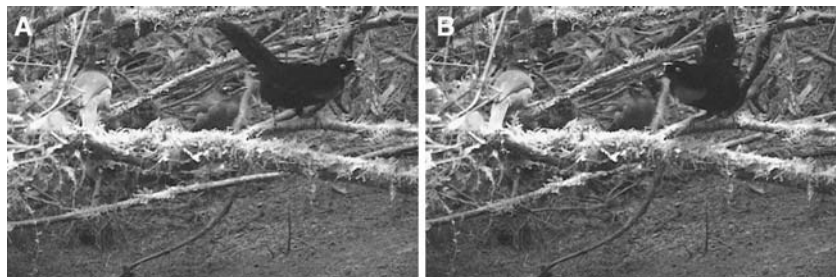


Fig. 7 Schematic diagrams depicting the lower-level relational structure for two male displays. The “root” nodes on the far left under the sub-class heading “behavior” corresponds to a terminal “tip” node of the same name in Fig. 3. The sequence of events reads from top to bottom. Dashed lines indicate components with some irregularity in the sequence

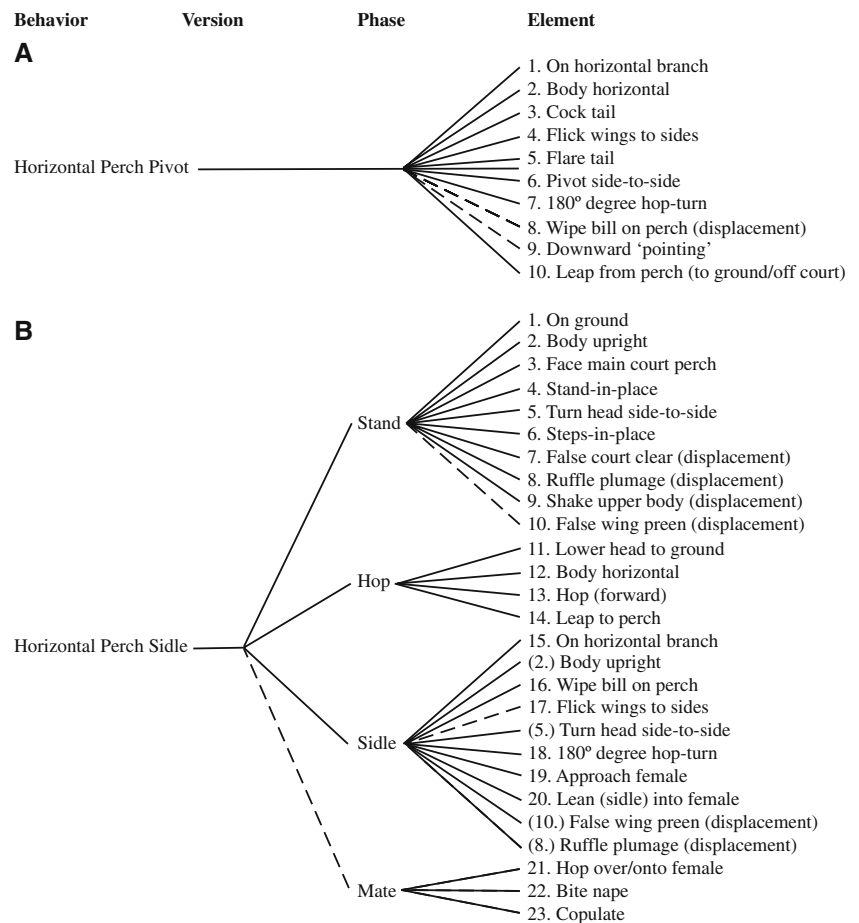


Table 2 Summary of quantified aspects of male displays

Display	Value
Horizontal perch pivot	
Display frequency (#/h)	0.19
Total observed	20
Bout duration (s) $n = 10$	11.52 ± 1.41
Pivot frequency (turns s^{-1}) $n = 10$	1.20 ± 0.13
Horizontal perch sidle	
Display frequency (# h^{-1})	0.67
Total observed	70
Stand duration (s) $n = 10$	6.87 ± 0.87
Hop duration (s) $n = 10$	2.10 ± 0.35
Sidle duration (s) $n = 10$	20.97 ± 3.83
Ballerina dance	
Display frequency (# h^{-1})	1.16
Total observed	121
Bow only (#bouts/total observations)	16/121
Stand duration (s) $n = 7$	6.16 ± 0.80
Bow duration (s) $n = 12$	3.07 ± 0.17
No waggle (#bouts/total observations)	19/121
Stand duration (s) $n = 10$	6.25 ± 1.34
Bow duration (s) $n = 10$	4.09 ± 0.14
Walk duration (s) $n = 10$	12.50 ± 1.12
Stationary waggle (#bouts/total observations)	86/121
Stand duration (s) $n = 25$	6.04 ± 0.55
Bow duration (s) $n = 25$	4.64 ± 0.31
Walk duration (s) $n = 25$	7.25 ± 0.81
Pause duration (s) $n = 25$	7.17 ± 0.26
Waggle duration (s) $n = 25$	8.00 ± 0.79

Values reported as the mean \pm SE where appropriate

Horizontal perch sidle (Figs. 8A–D; video_45966 to 45968)

A presentation display (Fig. 3). The male approaches and sidles up next to a female perched nearby. There

are 23 elements subdivided into four phases (i.e. temporal stages): Stand, hop, sidle, and mate phases (Fig. 4B). Quantified components summarized in Table 2. *Place*—stand and hop phases: court floor facing main court perch; sidle and mate phases: horizontal perch adjacent to female(s). *Posture*—stand phase: body upright (Fig. 8A); hop phase: body horizontal (Fig. 8B); sidle phase: body upright (Fig. 8C). *Action Patterns*—stand phase: stand-in-place, turn head from side-to-side (Fig. 8A), steps-in-place, false court clear, ruffle plumage, shake upper body, false wing preen; hop phase: lower head to ground, hop forward (Fig. 8B), hop on to perch; sidle phase: wipe bill on perch, flick wings open/shut, turn head from side-to-side, 180° hop-turns, approach female (Fig. 8C), lean into female (Fig. 8D); mate phase: hop over/on to female, bite nape; copulate. *Spatial Movement*—hop phase: movement across court in one direction until up on horizontal perch; sidle phase: lateral movement along perch to approach female. *Other Action Patterns*—false court clear; ruffle plumage; false preen; bill wipe.

Ballerina dance (Figs. 9–11; video_45954 to 45958)

The quintessential *Parotia* presentation display. Flank plumes are positioned around the body—resembling a ballerina’s tutu—as the bird performs an intricate dance. There are 30 elements, three versions (i.e. alternative forms: bow only, no waggle, and stationary waggle versions; Fig. 12) and five phases (stand, bow, walk, pause, and waggle; Fig. 12). *Place*—stand and bow phases: court floor facing main court perch; walk,

Fig. 8 Phases of horizontal perch sidle display (video_45966 to 45968): **A** stand phase, **B** hops-across-court phase, and **C** and **D** sidle phase

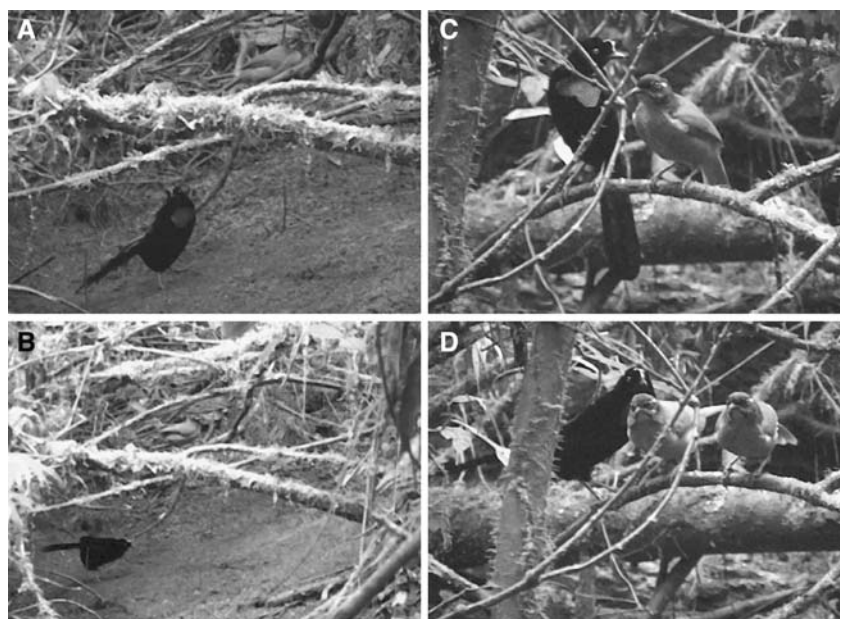
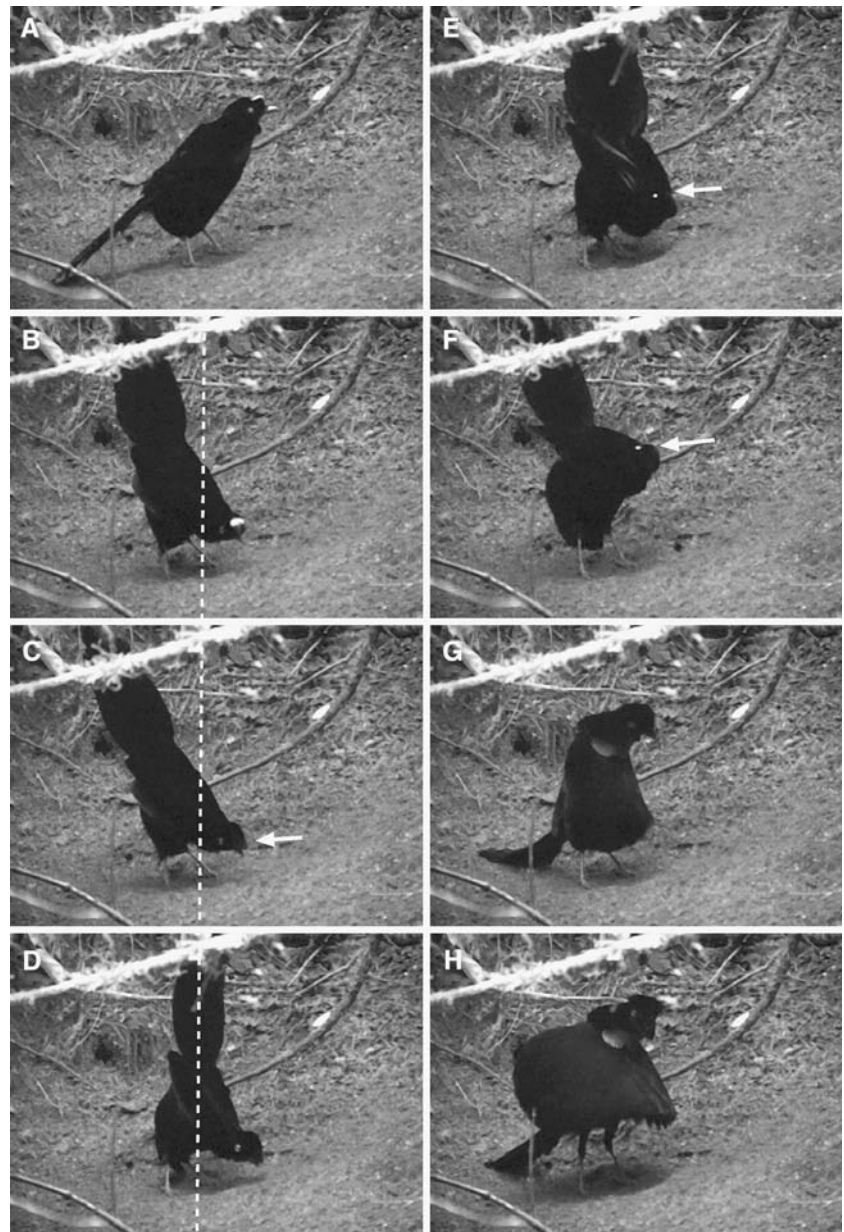


Fig. 9 Type II bow phase of the ballerina dance display (video_45958): **A** upright body posture, **B–D** head-to-ground bow with the range of motion covered in the lean-to-side illustrated with the dotted white line, **E** the head tuck (to wrist) with arrow pointing to flash of light reflecting from eye, **F** raise up (arrow still pointing to eye), **G** and **H** skirt formed from expansion of flank plumes



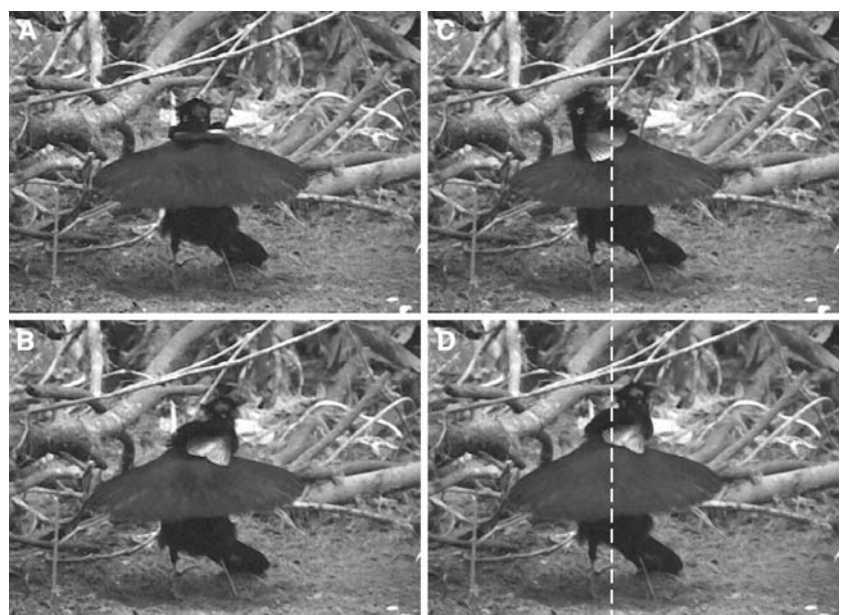
pause, and waggle phases: beneath main court perch. *Posture*—body upright during all phases (Fig. 9A). *Action Patterns*—stand phase: stand-in-place, turn head from side-to-side, steps-in-place, false court clear, ruffle plumage, shake upper body, false wing preen; bow phase: lower head to ground (Fig. 9B), move forehead tufts (Fig. 9C, see arrow), cock tail, lift up on toes, lean to side (Figs. 9B–D), tuck head (Fig. 9E), rise up (Fig. 9F, G), form skirt from flank plumes (Fig. 9H), move head wires; shake head; walk phase: walk forward/back (Fig. 10A), shake head,

change orientation (Fig. 10B); pause phase: stand in-place (Fig. 10C), crouch, sway head/upper body back and forth (Fig. 10C, D), lower flank plumes slightly (Fig. 10E), slowly lift body and “skirt” up, twitch “skirt” (Fig. 10F), move head wires to sides and back; waggle phase: plunge head (Fig. 11A), waggle head and neck (Fig. 11B–D), squat-and-rise, relax flank plumes. *Spatial Movement*—walk phase: walk from one end of court to beneath main court perch, rotate 180° to face origin. *Other Action Patterns*—false court clear; ruffle plumage; false preen; body shake; bill wipe.

Fig. 10 Walk and pause phases of the ballerina dance display (video_45956): **A** and **B** forward walking, **C** and **D** stand-in-place while shaking head and upper body, **E** squat with skirt lowered, **F** raise up with skirt lifted high and twitched when at the highest point



Fig. 11 Waggle phase of the ballerina dance display (video_45956): **A** head plunged into body (breast shield thrust up beneath bill; parallel to ground), **B–D** head wagged to left and right; the *dotted line* shows range of motion for the head and neck



Discussion

Significance of new observations

Before this study little was known about the courtship of *P. wahnesi*. Including data from both captive and wild birds the only behavior patterns previously recorded were three male displays:

- 1 twisting back-and-forth on a perch (Frith and Beehler 1998);
- 2 hopping-across-court (Coates 1990); and
- 3 a ballerina dance described as similar to that of Lawes’ parotia, *P. lawesii* (Coates 1990; Frith and Beehler 1998), but with a prominent tail-fanning component during the bow (Crandall 1940).

This study, by dissecting the “anatomy” of courtship, reveals the details of etho-phenotypic structure and shows that the courtship ethology of *P. wahnesi* is very complex. Observations of wild birds and analysis of digital video indicate that courtship and mating comprises eleven diagnosable behavior patterns organized within a highly structured framework (Figs. 3, 7, 12). Two behavior patterns described here, the hori-

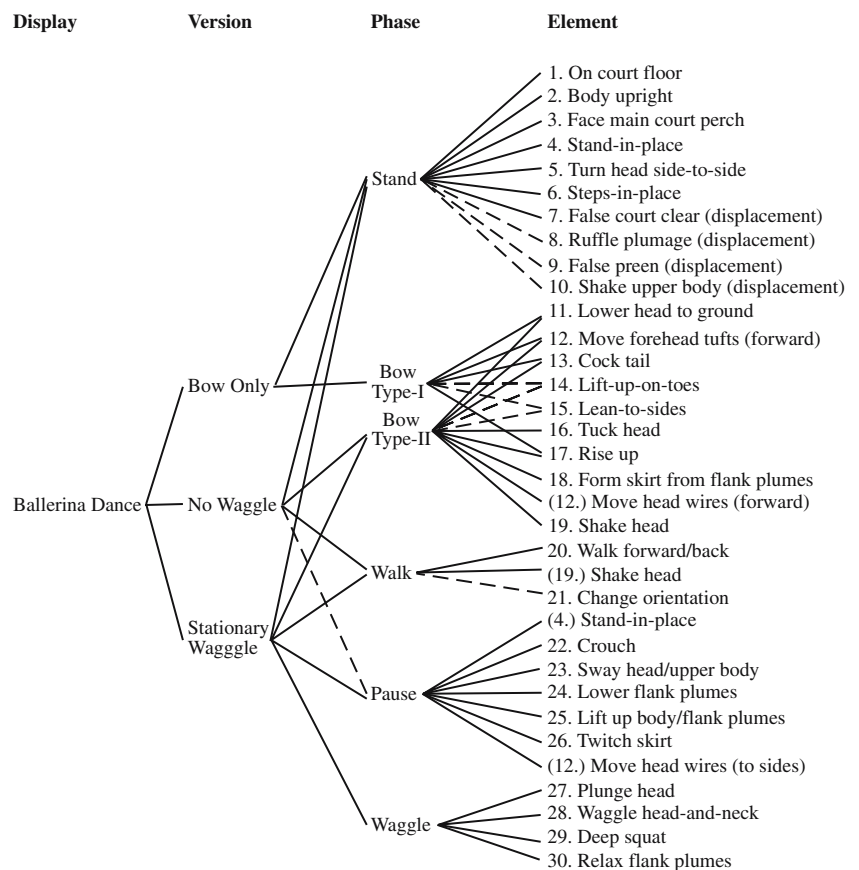
zontal perch pivot and the ballerina dance display, correspond to male displays described previously, although the ballerina dance described here differs from previous accounts in that it is more complex (Fig. 12) and does not include tail-fanning. The long tail is a focal point of the bow phase (Fig. 9B–F), but it was never fanned as described by Crandall (1940).

The third previously described behavior pattern, hops-across-court, is also described here, but was not found to be an independent unit at the level of a discrete display as previously implied (Coates 1990; Frith and Beehler 1998). Instead, the hops-across-court is an integrated component of a more complex display, the horizontal perch sidle (Fig. 7B). The significance of this observation is discussed below.

Structural organization and modularity

The entire courtship and mating phenotype of *P. wahnesi* comprises behavior patterns arranged within a complex etho-phenotypic structure comprising seven hierarchical levels (Figs. 3, 7, 12). Examination of the higher-levels of the phenotype hierarchy (Fig. 3) reveals that the structure of courtship and mating in *P. wahnesi* mirrors the higher-levels of the complex

Fig. 12 Schematic diagram depicting the lower-level structure of the ballerina dance display. The “root” node on the far left under the sub-class heading “behavior” corresponds to the terminal “tip” node of the same name in Fig. 3. In general, the sequence of events reads from top to bottom. *Dashed lines* indicate components with some irregularity in the sequence



phenotype of *P. carolae* (Scholes 2006). In this arrangement the highest-level unit is the courtship and mating phenotype itself, which is a sub-component of the entire *P. wahnesi* phenotype. Within this highest-level unit, there are eleven discrete behavior patterns that are at the level commonly recognized as the focal units of organismal behavior (i.e. “displays,” “courtship behavior,” etc.). These eleven behavior patterns are partitioned between the sexes, between two context-dependent categories, and among nearly the same suite of functional categories (Fig. 3).

Although some aspects of the higher-level structure were expected to be the same as for *P. carolae* (e.g. sex-specific and display/non-display behavior), the finding of virtually the same suite of functional categories is surprising, given that *P. wahnesi* has just eleven behavior patterns compared with 20 for *P. carolae* (Scholes 2006). The approximately same number of functional categories (*P. carolae* has one additional category), but with fewer total behavior components, implies less redundancy, and therefore less overall complexity, for *P. wahnesi* compared with *P. carolae*. For example, whereas female *P. wahnesi* have single-mate sampling and solicitation behavior (Fig. 3) *P. carolae* females have two; whereas male *P. wahnesi* use one enticement display *P. carolae* males use three, etc. The only exception to this pattern is in the displacement behavior category, in which *P. wahnesi* has exactly the same set as *P. carolae*. The significance of the two species having the same suite of displacement behavior components is unknown, but these behavior patterns are probably plesiomorphic.

As with *P. carolae*, the lower-level structure of male displays contributes the most to overall complexity (Figs. 7, 12). At lower-levels (examined for male displays only), behavior patterns comprise smaller units and sub-units at three hierarchical levels. At the lowest level (i.e. elements), 46 distinct units were found. The finding of 46 elements is extremely surprising, given that they comprise just three behavior patterns. In comparison, at the same level within the courtship phenotype of *P. carolae* a total of 58 distinct elements were discovered, but those 58 elements are distributed among seven behavior patterns (Scholes 2006).

One implication of these findings is that the courtship of *P. wahnesi* comprises modular units at different levels of organization. Evidence for modularity comes from the discovery that the courtship and mating phenotype comprises discrete hierarchically arranged units that are differently used in arrays constituting additional semi-autonomous units at higher levels of integration. For example, the basal units (i.e. elements) examined here are integrated into larger units that

form the distinct behavior patterns at the level of independent displays (i.e. the horizontal perch pivot) but also comprise behavior patterns that are the semi-autonomous components of behavior patterns at higher levels of integration within the phenotypic hierarchy—i.e. the different phases and versions that constitute the horizontal perch sidle and ballerina dance displays.

Phases are interesting because they mark the discrete temporal boundaries around the subset of elements that comprise otherwise continuous behavior patterns. For example, the sequence of events comprising the horizontal perch sidle (Fig. 7B) may be interrupted before running to completion, but the ending point would correspond with the sequence of integrated elements that mark the boundary of a phase. Furthermore, if begun again, the display would begin from the initial phase, not a later one in the sequence. This implies that even though the horizontal perch sidle is a stand-alone unit, it nevertheless comprises semi-autonomous subunits with less sub-independence. In other words, the later phases in the sequence do not occur independently of the earlier ones.

The major exception to the extent of sub-independence for the phases-as-units in the horizontal perch sidle display is the combination of elements constituting the stand phase. This combination of elements seems to have a fairly high level of autonomy, because the elements are recurrent in other contexts. For example, the stand phase is a component of all three versions of the ballerina dance display (Fig. 12). Because the repetitive employment, or recurrence, of units is a hallmark of modular design (Raff 1996; West-Eberhard 2003), the fact that the stand phase recurs within different behavioral units of the same phenotype provides evidence of modularity in the courtship phenotype of *P. wahnesi*.

As is observed for *P. carolae* (Scholes 2006), modularity is also evident at levels of integration higher than that of phases. Versions, for example, result from the differential deployment of the sequence of phases constituting the entire behavior pattern. For example, the three versions of the ballerina dance display are each semi-autonomous units that employ different subsets of the five phases that make up the overall behavior pattern (Fig. 12). The simplest version, the bow only, comprises the first two phases in the sequence: the stand and bow-type I phases. The bow-type I is an alternative form of the bow phase in which the complete sequence of elements has been abbreviated (Fig. 12). At the other extreme is the stationary waggle version, which comprises of all the phases.

General conclusions and broader significance

Comprehensive descriptive studies designed to illustrate organizational structure of complex ethological phenotypes are integral to the study of animal behavior not only because they inform us about interesting and important aspects of a species' natural history, but because they also have the ability inform us about the inherent biological properties that underlie the creation of organismal form. Birds of paradise, for example *P. wahnesi*, are an extreme example of how evolutionary processes like sexual selection can create extremely complex ethologically based phenotypes, for example the courtship phenotype described here, but understanding how this complexity originates and evolves requires detailed information about what, exactly, the phenotype is made up of (i.e. its "anatomy" or etho-phenotypic structure). This study and a previous one (Scholes 2006) indicate that *Parotia* phenotypic complexity can be at least partly attributed to the modular organization of the units that comprise courtship. When similar data are available for other species, comparative studies can be conducted to examine the role of these modular units through evolution (Scholes in preparation) and thereby enhance the structure-based view of behavior common to early ethologists in the light of modern ideas about the evolution and development of organismal form.

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