

RESEARCH ARTICLE



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The Display Behavior of Sub-Adult Greater Bird-of-Paradise (*Paradisaea apoda*): A Learning Process from an Adult?

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ABSTRACT

The Greater Bird-of-Paradise (*Paradisaea apoda*) is a bird that performs a courtship display (lekking) to attract females during the mating season. The objective of this study was to examine the display behavior of adult and sub-adult males on lek trees as a learning process by a sub-adult and identify the lek trees. The research was conducted in the Tunas Timber Lestari Ltd. Production Forest in central mainland Papua, in a non-breeding season. After a lek tree was found, a video recording was conducted. Analysis was performed from the video. The lek tree was an emergent species with a dense canopy. An adult male was observed to perform a dance display in front of sub-adult males, even in the absence of females. When adult males performed display, the sub-adult were observed the adult males in an upside-down position. The sub-adult also danced, but not as complete as the adult, suggesting that there was a learning process by the sub-adult. This study revealed that the sub-adult/young males of the bird-of-paradise has the ability to dance inherit from their fathers, and then perfect the dance through practice and watching adults. The lek tree surely need to be protected for the survival for this species.

Introduction

The Greater Bird-of-Paradise (*Paradisaea apoda*; Family: Paradisaeidae) is an endemic bird species on Papua Island. It is distributed in the southern part of the Jayawijaya Mountain range, mostly in Indonesian Papua and on Aru Island, a satellite island in the western part of Papua [1]. As a member of the Paradisaeidae family, the Greater Bird-of-Paradise also performs a complex and fascinating display, a ritual dance conducted on a lek tree where males gather to do the lekking to mate with females [2]. The lek tree of the greater bird-of-paradise commonly consists of horizontal tree branches with an approximate diameter of 8 cm, positioned at an elevation more than 20 m from the ground, and situated beneath a moderately dense canopy [3]. The most well-known feature of the Greater Bird-of-Paradise is the extraordinary, magnificent plumage of the male bird, which is important for dancing and is fully developed during the breeding season. In the non-breeding season, the colorful, bright, and shiny plumage slowly molts [4]. The female Greater Bird-of-Paradise is strikingly different from that of males; it has a plain brown color [5].

Research on the display behavior of this species in the last ten years is scarce, and thus, some older publications [6–8] are still used as references in this paper. Some published papers were available for the closest kin of the genus Paradisaea [9], namely the Lesser Bird-of-Paradise (*Paradisaea minor*) [10–12], which is distributed along the northern coastal area of Papua, including small adjacent satellite islands [1]. Display behavior in the greater bird-of-paradise is typically associated with the breeding season, although previous research [6] has suggested that this display behavior could occur throughout the year. In general, display behavior is influenced by two factors, namely, internal factors (i.e., genetics, inherited by parents) and

Corresponding Author: Raka Aditya Pramunandya 🖄 raka.aditya95@gmail.com 🗅 Tropical Biodiversity Conservation Study Program, Graduate School, IPB University, IPB Darmaga Campus, Bogor, Indonesia.

© 2024 Pramunandya et al. This is an open-access article distributed under the terms of the Creative Commons Attribution (CC BY) license, allowing unrestricted use, distribution, and reproduction in any medium, provided proper credit is given to the original authors. Think twice before printing this journal paper. Save paper, trees, and Earth! external factors (i.e., environmental factors, obtained after birth) [13], with one common external factor being influenced by other individuals, including young and adult individuals [14]. During the culmination of the display, the female selects the preferred male (presumably males with an appropriate dance) for the copulation process [15]. After copulation, the female lays eggs, incubates, and raises the chicks by herself [7]. More detailed information on the nesting behavior of the greater birds-of-paradise (including the number of eggs, incubation period in the wild, and weaning period) is virtually almost not unavailable.

The only indirect information about nest selection by the female parent was on a large and dry fern plant that patches tall trees [16]. Certainly, in the lek breeding system, the female was responsible for raising the young, without the presence of the males [17]. Meanwhile, dancing behavior was conducted by males. Some birds have the ability to 'learn' behaviors from other individuals or events in their environment, especially those related to vocalizations and movements as adaptive responses [18,19]. This learning and observational process aids juveniles in acquiring and imitating display movements upon reaching maturity during the subsequent breeding seasons [20,21], which might also occur in the Greater Bird-of-Paradise. The act of imitating movements from others is also called 'copying' [22]. The objectives of this study were to (a) examine the display behavior of adult and subadult males of the Greater Bird-of-Paradise on lek trees as a learning process by a sub-adult, and (b) identify lek trees and their characteristics. The research also tried to reveal whether there was a learning and copying process by the male sub-adult through watching the adult male performing the ritual dance.

Materials and Methods

Study Area

The study was conducted in the production forest (logging concession) of Tunas Timber Lestari Limited Liability Company (Ltd.), Boven Digoel Regency, South Papua Province, in December 2022, which corresponded to a rainy season. The study area was a mixed dry forest with an altitude range of 25 to 100 m above sea level. Tunas Timber Lestari Ltd. holds a Timber Forest Product Utilization Business Permit for natural forests. The company harvested timber by using a selective cutting system. To locate the Greater Bird-of-Paradise's lek, a preliminary observation was conducted from December 10 to 14, 2022.

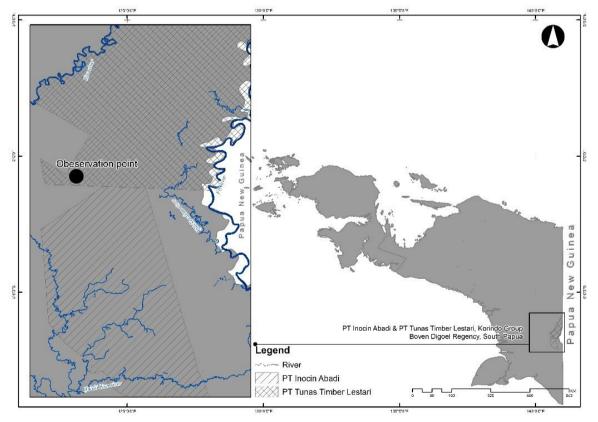


Figure 1. Research map depicting the observation point located in the mixed dry forest of Tunas Timber Lestari Ltd. concession area, bordering with Inocin Abadi Ltd.

The local people who had a good understanding of the forest conditions and lek tree location provided valuable information that aided in identifying observation points for birds and the locations of lek trees. The difficulty in finding a lek tree was because the peak breeding season, which normally occurs from July to September, had already passed. After four days of intensive searching through the forest, a lek tree was discovered in the Tunas Timber Lestari Ltd. concession area, near the border of another concession area of Inocin Abadi Ltd. (Figure 1). The location of the lek tree was not too far from the Inocin Abadi Camp, where some employees of the company (approximately 200 households) were accommodated. The trees were identified and measured, including the tree species, height, diameter at breast height (DBH), bole (branch-free) height, tree canopy diameter, leaf density, dominant species, canopy layer, forest floor density, clumps, emergent large trees, non-emergent large trees, disturbances, and distance to the village and road.

Observation of Bird Behavior

The first encounter with a group of bird parasites occurred on December 15, 2022, one day after the lek tree was discovered. Ten Greater Bird-of-Paradise individuals were recorded, comprising four females and six males that were not displayed. The following day, an observation blind was established at a distance of 15 m and a vision angle of approximately 45° from the eastern side of the lek tree. The constructed blind was covered with a black raincoat and nibung palm (*Oncosperma tigillariium*) leaves to minimize any disruption to the Greater Bird-of-Paradise throughout the observation period (Figure 2). Intensive observation of the behavior was conducted for two days, from 6:00 am to 11:00 am (local time), aligning with the peak display activity period in the morning until midday [12,16] afternoon and evening observations were omitted considering the anthropogenic disturbances caused by various human activities in the study area.

On the second day, when the Greater Bird-of-Paradise was not observed within an hour, a playback recording of the lek call was initiated to attract the bird to the lek tree. The playback recording stopped upon the bird's arrival. Individuals perched on the lek tree were documented through videographic recordings using a Sony Alpha 7 Mark II digital camera equipped with a Sony Gmaster FE 200–600 mm telephoto lens and a Sony 2x converter extension attached to a tripod. A total of 311 s of video recording was captured, but only 116 s (37.3%) contained the most important information and were used to analyze the behavior.



Figure 2. The observation blind was covered by a raincoat (left) and point of view from inside the observation blind (right).

Data Analysis

After emitting unnecessary sounds, the video data obtained were interpreted descriptively by examining individual morphology, timing of certain displays, interactions between individuals, and movements during displays and non-displays. The display movements of the Greater Bird-of-Paradise were categorized as wing pose, pump, bow, and dance [3] (Table 1).

 Table 1. Display lek behavior of the Great Bird-of-Paradise [3].

Display	Description			
Wing pose	Uphold the wings and tail for a couple of seconds and chirp "wauk".			
Pump	The body is lowered, wings are extended, the head is slightly lowered, legs are stretched out, the tail is moved rapidly, and movement from one branch to another is repeated.			
Bow	The head is lowered, the rear is arched, wings almost embrace the branch. It emits a 'baa' sound, the body remains stiff for up to a minute; this position marks the end of courtship. Females are not always present during this stage.			
Dance	Jumps and flapping wings, repeated.			

Results and Discussion

Lek Tree

A *Syzygium* sp. tree (family: Myrtaceae), located at coordinate 6°40'xx"S, 140°35'xx"E (exact location was hidden for a security reason) was identified as the lek tree for the bird-of-paradise in the study area (Figure 3). This tree emerged, although its diameter was not too large (Table 2) and the canopy had a moderately dense cover, allowing sunlight to penetrate. Despite its proximity to a residential area, the *Syzygium* sp. tree, serving as a lek site, was considered relatively safe because of its height. The presence of numerous large trees and shrubs around lek trees created a lush environment.



Figure 3. *Syzygium* sp. was used as a lek tree by two individuals: (left) tree structure, (middle) forest canopy, and (right) dense leaves of *Syzygium* sp.

Table 2. Description of the lek tree of the Greater Bird-of-Paradise located in the concession area of Tunas Timber

 Lestari Ltd.

Variable	Description
Location	Tunas Timber Lestari Ltd., Annual Logging Plan (<i>Rencana Kerja Tahunan</i>) 2021
Forest type	Dry mix forest
Lek tree species	Jambu (Syzigium sp.)
Diameter at breast high	30 cm
Tree height	30 m
Branch-tree section	10 m
Tree canopy diameter	8 m
Leaf bushiness	Medium
Dominant species	Jambu (Syzigium sp.)
Canopy layer	3
Floor forest density	Dense
Clumps	Not much
Emergent big tree	Many

Variable	Description
Non-emergent big tree	Not many
Disturbance	Close to the village, many footpaths, the sound of logging traffic can be heard, close to the daily activities of the local people.
Distance to the nearest village	500 m
Distance to the nearest road	430 m

The lek tree was located at a short distance from the residential area of Inocin Abadi Camp. However, the residents in that area generally did not disturb the Greater Bird-of-Paradise or the lek trees. Their activities mainly involved gathering firewood and hunting small animals such as wild chickens and Columbidae birds. Additionally, there was a small hut on the edge of the forest where residents received a signal in the evening. The lek tree was also relatively close to the main road; therefore, when logging vehicles passed by, noise and vibrations could be detected from the lek tree. Despite some disturbances in the surrounding area, the activity of the Greater Bird-of-Paradise seemed to continue.

Morphology of Bird Being Observed

The two Greater Birds of Paradise exhibited yellow heads with green throats, brown bodies, and wings, indicating that they were both male. Furthermore, the two focal birds could be differentiated by the color of their head feathers and the presence of ornamental feathers on their tails. One of the males had a dense feather coloring around his neck and body, complete head feathering, and two elongated ornamental tail feathers (or 'wires') measuring around 30 cm, which are the physical characteristics of an adult bird. However, the lack of side feathers indicates that the bird is not yet fully developed, and this male appears to be an older individual sub-adult. The other bird was identified as a younger sub-adult, with incomplete head feathering, less-developed elongated tail feathers, and a lack of clear separation between his neck and back feathers (Figure 4).

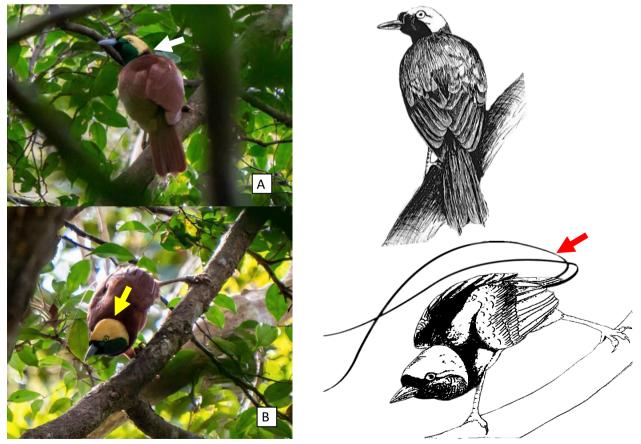


Figure 4. Young sub-adult male Greater Bird-of-Paradise *Paradisaea apoda* (A), indicated by incomplete yellow nape feathers (white arrow), and sub-adult birds (B), with characteristics by fully yellow nape feathers (yellow arrow) and ornamental tail feathers (red arrow).

Dance Behaviour

Two display behavior events were observed in this study. The first display was composed of a solitary young subadult male on a lek tree, whereas the second display event involved an 'older' subadult individual dancing in the presence of a young subadult male (Table 2). No females were present during the display behaviors of the young sub-adult and sub-adult birds. In this study, differences in display behavior between young sub-adult and sub-adult birds. In this study, differences of the completeness of display movements and the duration of each movement. All four display movements (wing pose, pump, bow, and dance) were observed in sub-adults, whereas only two display movements (wing pose and dance) were observed in young adults (Table 3).

Table 3. Two Displays of the behavior of two males of the Greater Bird-of-Paradise on a lek tree in the concession area managed by Tunas Timber Lestari Ltd.

Time	Seconds	Individual	Display	Description
08.25	0–17	Young sub- adult	Wing pose	Perch facing the 12 o'clock direction by spreading its wings and flapping them 8 times.
	18–21		Dance	Move the legs for 6 steps while the body moves in a circular motion forming the number 8, making the sound 'khaak' 7 times.
	22–50		Wing pose	Facing the 3 o'clock direction while spreading the wings 38 times.
	51–59		Perch	Facing to the right, the body faces 12 o'clock.
08.26	0–9		Perch	Nodding the head.
	10		Perch	Facing the right.
08.32	0–35	Young sub-	Perch	Head facing left, body faces the 12 o'clock.
		adult	Take of	Look around before flee.
08.39*	0–4	Young sub-	Perch	First, look upwards, then fly and perch on the branch above.
	5-25	adult	Perch	Look to the right and left, the body faces 6 o'clock.
	26–29		Grooming	Rubbing the feathers using a beak.
	30–39		Perch	Perching, facing the 6 o'clock.
	40–42	Sub-adult	Perch	Fly from the top branch of the tree.
	40-51	Young sub-	Perch	Look at the adult male and glance around twice, body facing the 6
		adult		o'clock direction.
	43–46	Sub-adult	Jump	Jump three times towards the young male, gaze directed towards the young male.
	47–49		Bow	Stay still and bow down for about 3 seconds, facing 2 o'clock.
	50–51		Rubbed beak	The body bows down faces 5 o'clock, beak rubbed against the side of the branch 6 times.
	52–54		Pump	The body bows down face, legs spread open, head pointing downward, moving by hopping downward.
	52–91	Young sub- adult	Inverted perch	Seeing an adult male with an upside position.
	52–54	Sub-adult	Dance	Wings flapped, legs spread open, and tail raised.
	55–56		Pump, wing	The body bows down facing the 6 o'clock direction, legs spread open,
	57–58		pose, bow	head pointing downward, moving by hopping slowly uphill 3 times, and
	59–60			making the sound 'choagh' 2 times.
08.40*	1–34		Dance	The head bows down, slowly flapping wings 40 times, then hopping 30 times and making the sound 'choagh' 13 times.
	32–33	Young sub- adult	Take off	Look at the adult male and the surroundings, then fly.
	35–42	Sub-adult	Perch	Looking around, take a rest with fast breathing.
	43-50		Jump	Hoop to branch above.
	51–54		Jump	Move to the smaller branch below, unexpected another individual is passing by.
	55–56		Take off	Fly and glide downwards with another individual on the left side.

*interaction between young sub-adult and sub-adult of the Greater Bird-of-Paradise

From 08:39:40–51, the sub-adult Greater Bird-of-Paradise landed on the same branch as the young sub-adult male. After landing, the sub-adult male immediately displayed in front of the young sub-adult male who promptly observed the sub-adult male. At the same time (08:39:52–91), the sub-adult male danced and the young sub-adult male perched upside down (inverted). When the young sub-adult male perched in an inverted position, his entire body was not visible because of the thickness of the foliage, but he continued to

gaze at the displayed sub-adult male. The lek movements of the young sub-adult male were fewer than those of the sub-adult male, with no pump and bow movements observed in the sub-adult male (Figure 5). However, in the wing pose movements, young males had more sessions and longer movement durations. There were distinct differences in movement between the young subadult and subadult males, where the subadult males had more refined display abilities (Table 4).

Table 4. Differences in display behavior by young sub-adult and sub-adult males of the Greater Bird-of-Paradise in the study area

Display behavior	Young sub-adult male	Sub-adult male
Wing pose	Observed 2 times, total duration 40 seconds	Once, for 1 second
Pump	Did not observe	Once, for 6 seconds
Bow	Did not observe	Twice, total duration 2 seconds
Dance	Observed 1 time, total duration 3 seconds	Twice, total duration 36 seconds

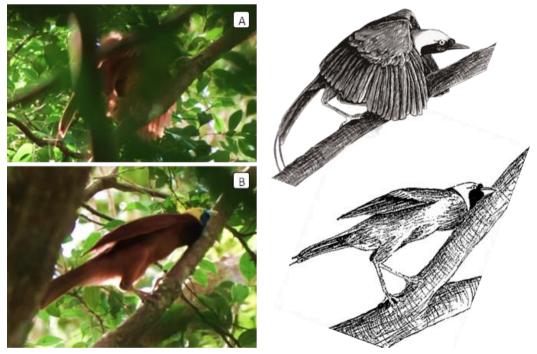


Figure 5. Display of sub-adult male Greater Bird-of-Paradise: wing pose (A) and bow (B).

Learning the Dance Steps from An Adult Bird

This study is the first to report the behavior of the younger sub-adult Greater Bird-of-Paradise, which learned and imitated a display dance from an 'older' sub-adult male bird in a non-breeding season. There was a hypothesis that "young males" (of the bird-of-paradise) inherit those dance steps from their fathers, and then refine them through practice and watching adults [23] (Figure 6). Although the hypothesis for the bird-of-paradise has not yet been written in a scientific paper, the process of watching and practicing ritual dance has been reported in some other bird species, such as in Java sparrow (*Lonchura oryzivora*) in captivity [24], cranes [25], and golden-collared manakin (*Manacus vitellinus*) [26].

In the Java sparrow observed in captivity, the young bird repeatedly practiced courtship dance from early life, a practice that was needed for motor learning and vocal-motional coordination [24]. Similar to the Java sparrow, the bird-of-paradise may have learned to display because it was released from its mother's care or during its juvenile phase. In another bird group, cranes (family Gruidae), it was found that the sub-adult bird also dances as a play behavior when performed in a non-breeding season [25]. Meanwhile, in the Golden-collared manakin, adults initially provided examples of behavior that were subsequently imitated by a young bird [26]. In the Greater Bird-of-Paradise, chicks were raised by their mothers without any interference from the father [9]. Therefore, the ability to dance, at least in some important steps, is an innate behaviour inherited from fathers. To perfect ritual dance, the sub-adult bird needs to learn and practice from the adult.



Figure 6. Young sub-adult male Greater Bird-of-Paradise (on the right) observing the dance of the 'older' sub-adult male *P. apoda* (on the left). The young sub-adult-male served in an inverted position (highlight by a red circle).

As mentioned previously, the behavior of the young/sub-adult male observing the adult male's dancing or singing is a part of learning [24]. In this study, the young sub-adult male had the opportunity to watch the dance from a short distance. The 'older' sub-adult male was also seen to provide an example of dance steps to the young sub-adult, like the report of the manakin study, using the adult's incomplete breeding plumage [26]. The inverted position is a common behavior in bird-of-paradise species [12]. However, the behavior of observing another male display in an inverted pose has not been recorded previously. The behavior of the young male, both upright and upside-down, suggests that he was actively observing the adult male's display, which might be closely linked to learning. Earlier research McDonald and Potts [20] revealed that young individuals naturally tend to pay attention to other males doing something like singing or searching for food, as well as display.

This was evident during the breeding season when displays occurred at the lek site, and all adults and subadults gathered for both display and observing [7]. There was no information on the watching, learning, and practice of the sub-adult Greater Bird-of-Paradise on a lek tree during the non-breeding season. There is a good possibility that the sub-adult might be present in the lek tree during the breeding season, watching, and learning from adults from a distance (not on the main lekking branch, possibly practicing by himself), but did not participate in the dance aiming for copulation. Another possibility is that learning and dancing also occur during the non-breeding season, as revealed in this study.

The differences in display movements, in which the sub-adult male did not perform a complete display, could be because the young male had not yet fully mastered the display movements. This suggests that the male's dancing ability was influenced by external factors, such as learning. The display behaviors exhibited by both

males indicate a tendency among males of the Greater Bird-of-Paradise to engage in the display, especially during the mating season. Meanwhile, display or sexual activities outside the mating season are believed to be triggered by other factors such as hormones and calling [27,28].

The Selection and Safety of Lek Tree

The dance site of the Greater Bird-of-Paradise was near the Inocin Abadi Camp, which is frequently used by locals for various activities. There have been some reports [24,28], that the bird-of-paradise shows a reasonable tolerance to habitat changes and disturbances. This means that the Greater Bird-of-Paradise is relatively easy to hunt illegally from plumage. The trees used by the Greater Bird-of-Paradise lekking in Tunas Timber Lestari Ltd. concession area were relatively dense. However, video footage from camera traps at Inocin Abadi Ltd. (adjacent to Tunas Timber Lestari Ltd.) captured images of the Greater Bird-of-Paradise performing lek displays in the sparse tree canopy. Another footage shot on Aru Island also indicated that open lek trees engage in display behaviors, including copulation [29]. Information about the lek preferences of the Greater Bird-of-Paradise remains limited, and it is suspected that canopy density may not be the primary factor determining display site selection.

At the same time, it is possible that the practice exhibition will be held in a partially closed lek tree, as opposed to an open main lek tree. This might occur because dense lek trees are safe from disturbances and threats, but are not exposed in the event of a female's presence nearby. In some areas where birds dance in an open environment, safety against illegal hunting must be maintained. Furthermore, in contrast to this study, a study on Aru Island identified three lek tree species: *Canarium vulgare, Myristica fragrans*, and *Pometia pinnata* [17]. All three species possessed a DBH > 30 cm and a height > 30 m, with relatively open canopies. This closely aligns with the characteristics of lek trees observed in this study. It is inferred that the selection of a lek tree by the Greater Bird-of-Paradise is not primarily based on its species but rather on its structural attributes.

Conclusions

The display behavior of the Greater Bird-of-Paradise in mainland central Papua (Indonesia) revealed that the display might have occurred during the non-breeding season. The behavior of young sub-adult male through watching a dancing 'older' sub-adult male reported in this study indicated that there was a learning, copying, and practicing process of the young/sub-adult in performing dance steps. This study strengthened the earlier hypothesis that young males of the bird-of-paradise have the ability to dance inherited from their fathers and still need to perfect the ritual dance through practice and watching the older male. Lek trees for practice tended to be more closed, indicating that safety was a priority. In contrast, the main lek tree was more open, prioritizing the possibility of mating. As the lek tree is crucial for the dance ritual and survival of this bird, its protection of the lek tree is necessary.

Author Contributions

RAP: Conceptualization, Formal Analysis, Methodology, Software, Visualization, Investigation, Writing – original draft; **AM**: Project administration, Supervision, Validation, Writing -review and editing; **YAM**: Supervision, Validation, Writing -review and editing **VC**: Resources, Funding acquisition.

Conflicts of Interest

There are no conflicts to declare.

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