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THE USE OF COURT OBJECTS BY LAWES' PAROTIA[1]

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Abstract. Males of Lawes' Parotia (*Parotia lawesii*), a lek-breeding bird of paradise, collected objects at their terrestrial display courts. These included shed snake skin, mammal scats, chalk, mammal fur, feathers, and bone fragments. The objects were not used by males in their courtship display but were rubbed on the display perch and may have had indirect effects on display. Females searched for and took the objects when visiting courts, and males stole them from each other and placed them at their own courts. Experiments showed that objects were removed quickly by females, usually within 24 hr, and once taken, they were not brought back. Females only took objects during the nesting season, and we suspect that females used the shed snake skin as nest-lining material and ate the chalk as a mineral supplement. Collection of the items was not related to mating success in males but may have influenced female visitations.

Key words: Lawes' Parotia; bird of paradise; court objects; display objects; mating behavior; Papua New Guinea.

INTRODUCTION

The purpose of this paper is to describe an unusual behavior in Lawes' Parotia (*Parotia lawesii*), a montane species of bird of paradise (Paradisaeidae). Males collected natural objects in the forest and placed them at their terrestrial court sites. This behavior is similar to the collection of display ornaments by male bowerbirds (Marshall 1954, Gilliard 1969, Cooper and Forshaw 1977, Diamond 1986) except that in *P. lawesii,* males did not use the objects in display and each type of item was removed by females. Collection of the objects by females was restricted to the breeding season and we believe they were important in reproduction.

Lawes' Parotia occurs in montane, rainforest habitats from 1,000 to 2,200 m altitude in eastern Papua New Guinea (Gilliard 1969, Schodde and McKean 1973, Beehler et al. 1986). The species is almost totally frugivorous (Beehler 1983, Beehler and Pruett-Jones 1983, Pratt and Stiles 1985), feeding on canopy and subcanopy fruits. Males display terrestrially at court sites which they clear and actively clean, maintain, and defend from other males (Schodde and Mason 1974, Beehler and Pruett-Jones 1983). Males mate promiscuously and do not assist females with parental duties (Pruett-Jones 1985).

METHODS

The data presented here were gathered as part of a long-term study of lek evolution in *P. lawesii* (Pruett-Jones 1985). Fieldwork was conducted on Mount Missim, Morobe Province, from August to December 1980, and August 1981 to December 1983 (see Pruett-Jones and Pruett-Jones 1982, 1986). We worked on an area composed of primary, montane rainforest approximately 1,000 ha in size, from 1,300 to 2,200 m altitude. This area encompassed the entire altitudinal range of adult male *P. lawesii* on Mount Missim and between 25 and 32 males held courts on the study area each year. In this population, the majority of courts were spatially clumped at lek sites but approximately one-third of the males each year displayed solitarily (Beehler and Pruett-Jones 1983, Pruett-Jones 1985). A total of 144 birds were individually color-banded on the study area.

Each season from 1981 to 1983 was divided into regular sampling periods of 3 weeks (1981) and 2 weeks (1982, 1983). Courts were active for up to 10 months a year, yielding a total of 49 sampling periods over the three seasons. During each period, all courts were checked for activity and the presence of objects. A total of 21, 23, and 20 courts were monitored in 1981, 1982, and 1983, respectively.

Use of the items by males and response to objects by conspecifics were quantified during behavioral samples from hides set near courts. Samples were 4.0 to 5.5 hr in length, conducted throughout daylight hours, and most or all males

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in the population were sampled each period. We report data from 920 behavior samples (total of 4,424 hr) on 19, 23, and 22 adult males during 1981, 1982, and 1983, respectively. The data from one of the males studied in 1981 were deleted in the analysis of mating success due to insufficient sampling of that individual.

For analysis, we calculated three measures of the collection of objects by males: (1) the proportion of sample periods during which males had objects at their courts, (2) the proportion of behavior samples during which males brought in items, and (3) the actual rate of collection (objects/10 hr of observation). These variables were strongly intercorrelated ($P < 0.005$ in each regression).

During behavior samples we placed various objects at courts to determine any preferences by males for color or type. We offered blue, green, red, white, and yellow fruits known not to be eaten by *P. lawesii,* fruits identified as part of the species' diet, flowers, and white lichen.

At a central lek we conducted experimental offerings of objects to quantify rates of disappearance. For each offering, the objects were placed at all active courts (nine in 1982, six in 1983) at 06:30 on day 1. Then the courts were checked, and the number of objects recorded three times, at 10:00, 14:00, and 17:30, that day and then four times on day 2. In the snake-skin experiment, courts were also checked on day 3.

Two offerings of snake skin were conducted, from 20–22 October 1982 and from 25–26 January 1983. Four small pieces, each approximately 16 × 8 mm in size, were placed at each court. Because males quickly tore the snake skin into smaller pieces, we counted the number of whole pieces and whole-piece equivalents (an estimate of the number of pieces represented by the many smaller pieces). The offering of mammal scats was conducted from 22–23 November 1983. The scats offered were found in the forest at den sites of opossums (*Phalanger vestitus* and *P. orientalis*) and were of the same type and size found at courts naturally. Three scats, each marked with a small white dot, were placed at each court. Two experiments with standard chalkboard chalk were conducted, from 27–29 November 1982 and from 28–29 November 1983. Three pieces of chalk, broken into small pieces 5 to 8 mm on each side, were placed at each court.

During additional work on the study area in 1986, a sample of chalk was collected from a court and sent to a commercial laboratory for spectroscopic analysis of trace elements. The analysis technique used was inductively coupled plasma-atomic emission spectrometry (methods 43.292–43.296 and 4.A01–3.A04, Official Methods of Analysis, 14th Edition, 1984, and 1st Supplement, 1984, AOAC, Arlington, Virginia).

RESULTS

The courts of *P. lawesii* consisted of cleared areas on the forest floor and ranged in size from 0.5 to 20.0 m^2. Each court was cleared and maintained by only one male and individual males cleared from one to five courts (in our use of the term court, we are referring to the single or multiple sites that an individual male used for display). The court itself, but not the surrounding forest, was aggressively defended against conspecific males. Courts were cleared only under a suitable display perch which was a horizontal or slanting branch or vine, usually 1 to 3 cm in diameter, and approximately 0.5 m above the court. During the breeding season, males cleared all debris, e.g., leaves, bark, twigs, fungi, small stones, etc., off their court each time it was visited. Males also pulled leaves from small saplings at the court. Males did not clear away the objects discussed here. All display interactions and matings took place at the court.

OCCURRENCE AND SEASONALITY OF OBJECT USE

Several kinds of objects were recorded (Table 1). Shed snake skin and mammal scats were most common, followed by chalk, fur, feathers, and bone fragments. Other objects seen at least once, but not regularly observed, were small rootlets, snail shells, and pieces of clear plastic wrapping.

We did not identify the snake skin to species, but skins of large pythons were the most frequently seen. Most mammal scats were 5 to 7 mm in diameter and 35 to 40 mm long, composed of compacted plant material and insect parts, and thought to be those of opossums (*Phalanger* sp., *Pseudocheirus* sp). Scats of forest wallabies (*Thylogale bruijni* and *Dorcopsulus vanheurni*) were infrequently observed at courts. The chalk was collected by males as small pieces, about 10 mm across, from landslides in the forest with exposed mineral veins. The fur appeared to be either shed fur or actual remains (skin with fur attached) of small mammals. The feathers

TABLE 1. Presence of objects at courts.[1]

	Periods during which courts had objects[2]		Active courts where objects were found[3]	
	All periods *n* (%)	Breeding season *n* (%)	All periods *n* (%)	Breeding season *n* (%)
Total	49	27	675	491
Any object	33 (67.4)	25 (92.6)	201 (29.9)	171 (35.0)
Snake skin	31 (63.3)	23 (85.2)	93 (13.8)	74 (15.1)
Mammal scat	30 (61.2)	24 (88.9)	120 (17.8)	99 (20.2)
Chalk	17 (34.7)	14 (51.8)	37 (5.5)	33 (6.7)
Fur	7 (14.3)	7 (25.9)	9 (1.3)	9 (1.8)
Feathers	3 (6.1)	3 (11.1)	3 (0.4)	3 (0.6)
Bone	1 (2.0)	1 (3.7)	1 (0.2)	1 (0.2)

[1] Data from 1981, 1982, and 1983 combined.
[2] Courts were checked during 49 sampling periods overall and 27 periods during the time of matings each year. Thus, during 31 (63.3%) periods, at least one court of those checked had snake skin present.
[3] Considering each court separately each period, there was a total of 675 courts checked for objects, 491 during the time of matings. As objects were removed quickly from courts by conspecifics, it is unlikely that they were ever counted twice in successive periods.

were small and colored (not from *P. lawesii*). The bone fragments were pieces of jawbone from small mammals.

Concentrations (ppm) of trace elements of the chalk sample that was analyzed were as follows: Ca—270, P—182, Mg—237, Na—4512, Al—<35.4, Ba—<35.4, Fe—29.3, Sr—<35.4, B—<35.4, Cu—1.32, Zn—1.27, Mn—<0.88, Cr—<35.4.

Only adult males collected the items; on the three occasions when immature males maintained courts, they did not bring in objects. Most, but not all, males collected objects. Individual males had objects at their courts on an average of 29.9% of the occasions that we visited the court over the entire year, 35.0% during the breeding season (September to February; Table 1). During all 3 years combined only four (6% of total numer) males were never seen to have objects at their courts or to bring them in during behavior samples. Both solitary and grouped males collected objects at the same frequency.

Our data on year-round seasonality of activity at courts and use of objects is most complete for the period April 1982 to March 1983 (Fig. 1). Some courts were active throughout the year (Fig. 1A), with individual males active for an average of 24 weeks. With the exception of the early season, from April to June and then again in August, males collected objects throughout the period of court activity (Fig. 1B).

The retrieval of objects by females was restricted to the nesting period (Fig. 1C). In late August, before matings started, females did not take objects despite the fact that some courts had them. Females were observed taking objects from

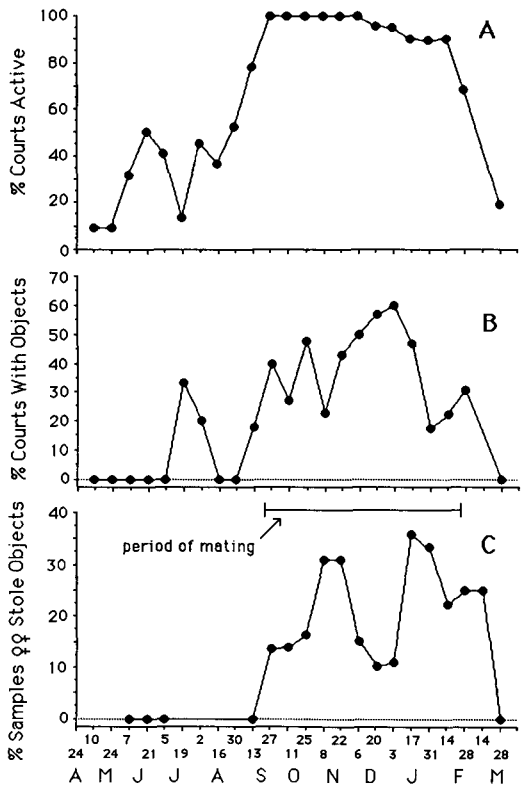

FIGURE 1. Seasonality of court activity (A), occurrence of objects at courts (B), and the removal of objects by females (C). The data for Figure 1A and 1B were gathered during regular court checks and those for Figure 1C during behavior samples. In Figure 1C, intervals with no data points represent periods during which no behavior samples were conducted. The time period was April 1982 to March 1983.

TABLE 2. Collection of objects by residents and removal by conspecific males and females.[1]

	Number of behavior samples[2]					
	The resident male retrieved objects		Females took at least one object		Conspecific males took at least one object	
	n	%	*n*	%	*n*	%
Any object	206	22.4	181	19.7	103	11.2
Snake skin	119	12.9	139	15.1	66	7.2
Mammal scat	86	9.4	30	3.3	36	3.9
Chalk	9	1.0	8	0.9	1	0.1
Other objects (combined)	21	2.3	16	1.7	6	0.6

[1] Data from 1981, 1982, and 1983 combined.
[2] A total of 920 behavior samples was conducted; percentages were calculated with reference to this value.

courts during approximately one-fifth of all behavior samples (Table 2).

Comparable data to that in Figure 1C for the 1983 season also indicated that females did not take objects prior to the nesting season. During June, July, and August 1983 an average of 21% (range = 0–60%) of active courts had objects but during only one of 17 behavior samples was a female seen to collect items from a court.

USE OF OBJECTS BY MALES AND RESPONSE OF CONSPECIFICS

Males that were more active at their courts collected more objects. There was a significant, positive correlation between attendance of the court by males (proportion of time during behavior samples that males were present at their court) and the rate of collection of objects ($n = 63$, $r = 0.490$, $P = 0.001$). On arrival at the court with objects, males typically rubbed them along the display perch and the vertical, bare saplings before placing them on the court. The objects were held at the end of the male's bill and then methodically rubbed up and down the perch or sapling. Rubbing behavior became more frequent and intense if the male brought in several items at once, e.g., several pieces of snake skin. Males rubbed snake skin along their perch for as long as 20 min. The rubbing behavior was not, however, an actual display; males neither picked up the objects during interactions with females, nor in any way obvious to observers tried to draw the attention of females to the objects.

The section of the display perch directly above the court was often smoother and shinier than the remainder of the branch of vine. We could not detect whether the rubbing of objects made the perch more visible or left an odor, except with respect to the chalk. Chalk marks—wide, white streaks along the perch—were noticeable from 10 to 15 m away.

Males rearranged the location of objects at their court throughout the day. Objects were not placed in any regular fashion or in one particular area but they were generally placed towards the center of the court and in clear view from the display perch. The objects were never hidden and the males did not eat them. For males that maintained more than one court, the objects were invariably placed at the site used most often for display.

Objects were not always present at courts (Tables 1, 2) but visitors behaved as if they were searching for them. Visitors dropped from the display perch to the court and then hopped back and forth with their head downwards scanning the surface. If an object was present, the visitor invariably took it. Both males and females visited courts when the resident was present as well as when the resident was absent. If the resident was absent, the visitors went directly to the court, collected whatever objects were there, and left immediately. Banded females were observed to return repeatedly to a given site to retrieve all available snake skin if a large amount was present. When in attendance, the resident male immediately chased females away if the females tried to land on the surface of the court as if to steal the objects. Visiting males were usually chased away whether or not they appeared to be trying to steal objects. When conspecific males did take objects they would fly to their own area and rub and arrange the objects as described above.

EXPERIMENTAL OFFERINGS

Of the items placed at courts during behavior samples, all inedible fruits, regardless of color, were either tossed off the courts as soon as the male arrived or, in a few cases, ignored. No positive responses (rubbing along the display perch)

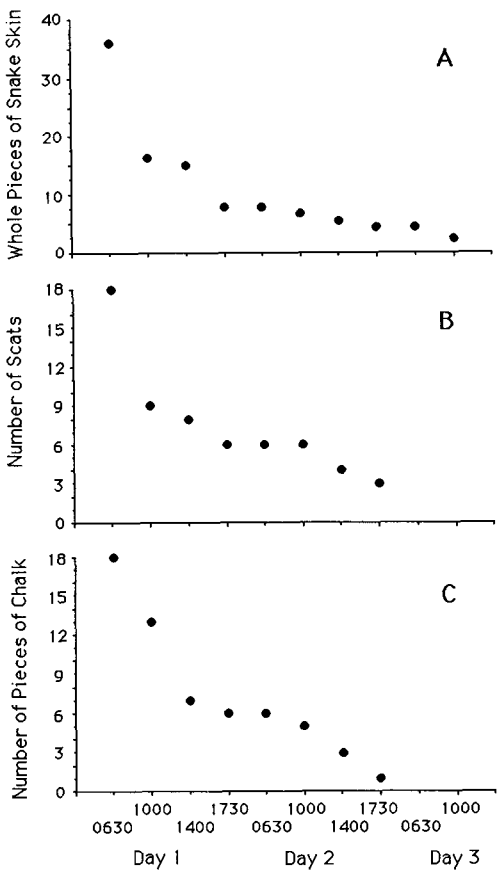

FIGURE 2. Removal by females of objects offered at *P. lawesii* courts: A. Number of whole pieces, or equivalents, of shed snake skin (four pieces placed at each of nine courts); B. Mammal scats (three scats placed at each of six courts); and C. Chalk (three pieces placed at each of six courts). See Methods for additional details.

were seen. The edible fruits were eaten (five of 25 fruits offered at eight courts), tossed off the court (19 of 25), or in one case, ignored. The flowers and lichens were also tossed off the court. Snail shells were tossed off at one court and ignored at another. With respect to these same items, females showed a response only to the edible fruit (one female ate one fruit). None of the items were taken by females or by conspecific males.

The results of the snake skin, mammal scat, and chalk experiments are illustrated in Figure 2. The double experiments with snake skin and chalk each yielded similar results, and with respect to both objects we report the results from only one offering. The number of items present declined rapidly during the morning of the first day and then more slowly during the afternoon and on the second day (Fig. 2). More than half of the snake skin and mammal scats were taken within 4 hr of their placement at courts. By the end of the second day, only 10 to 15% of the original number of objects remained.

The lek where experiments were conducted was more than 1 km from the nearest lek and over 500 m from the nearest solitary court. Males did not make interlek visits and the male displaying solitarily was seen at the study lek only once during the 1982 season. Thus, reduction in the total number of objects at the lek during the experiment was due to loss through females taking the objects, not from outside males stealing them. The number of objects never increased between court checks and there was no evidence that males retrieved natural objects during the time of the experiment.

COURT OBJECTS AND MATING SUCCESS OF MALES

Elsewhere (Pruett-Jones 1985; Pruett-Jones and Pruett-Jones, unpubl.) we present data on mating success of males and female choice in *P. lawesii.* All males received female visitors, but not all males mated. During 1981, 1982, and 1983 respectively, 7 of 18 (38.9%), 7 of 23 (30.4%), and 9 of 22 (40.9%) males obtained matings. For 1981 to 1983 combined, successful (mating at least once) males (n = 24) averaged a collection rate of 0.8 objects/10 hr of observation (SD = 0.5, range = 0–1.7). The mean rate of collection for unsuccessful (nonmating) males (n = 39) was 0.6 objects/10 hr of observation (SD = 0.5, range = 0–1.5; differences not significant, Mann-Whitney $U = 560$, $Z = -1.32$, $P > 0.10$). One of the four males that was never observed to collect objects did successfully mate. The collection of court objects correlated with the length of female visits, but not with the rate of female visitation or the mating success of males (Table 3). The rate of female visitation, the length of female visits, and the mating success of males were each intercorrelated with each other (Pruett-Jones and Pruett-Jones, unpubl.).

Six nest-site locations of *P. lawesii* were found during this study and work by T. K. Pratt between 1978 and 1980 (pers. comm.). Due to the height and inaccessibility of the nests, we could not verify whether females placed court objects

TABLE 3. Correlations between measures of collection of objects by males and female visitations and mating success.[1]

	% sample periods[2]		% behavior samples[3]		Rate of collection[4]	
	r	*P*	*r*	*P*	*r*	*P*
Rate of female visitation (females/hr of observation)	0.189	0.152	0.246	0.052	0.215	0.090
Mean length of female visits (min)	0.246	0.066	0.354	0.005	0.262	0.041
Mating success of male (matings/10 hr of observation)	0.078	0.559	0.022	0.863	0.023	0.860

[1] Based on the combined data from 18, 23, and 22 males studies in 1981, 1982, and 1983, respectively. *P*s < 0.05 are underlined.
[2] The proportion of sample periods males were observed to have objects at their courts.
[3] The proportion of behavior samples during which males were seen to bring in objects.
[4] The rate of collection (objects/10 hr of observation).

at or near their nests. The nesting biology of *P. lawesii* remains sparsely known.

DISCUSSION

Accounts and descriptions of courts of *P. lawesii* from other areas in Papua New Guinea are provided in Gilliard (1969), Schodde and McKean (1973), Schodde and Mason (1974), and Cooper and Forshaw (1977). These authors made no mention of objects at the courts. B. Bacchus reported (pers. comm.) shed snake skin at the courts of *P. lawesii* on Crater Mountain in Eastern Highlands Province. We suspect this behavior will be shown to be common in other populations as well.

Because males do not derive benefits from the objects themselves, it seems clear that males collect them for females. Moreover, given that the removal of objects by females is restricted to the period of mating and nesting, we believe that all objects were used in some context related to reproduction. We suspect that females used the shed snake skin as nest-lining material. The repeated and frequent visits of some females to courts to collect snake skin when large amounts were offered suggested to us that they were taking it somewhere, perhaps a nest, and then returning for more. We were, however, unable to locate a nest which could be observed or closely examined and cannot confirm this. Hartert (1910, cited in Gilliard 1969) provides a description of a nest of *P. lawesii* but there was no mention of snake skin.

The Paradise Riflebird (*Ptiloris paradiseus*) and Queen Victoria's Riflebird (*Ptiloris victoriae*), relatives of *Parotia lawesii* endemic to Australia, are known to use shed snake skin as nest lining. Campbell (1974) provides a photograph of a nest of *P. paradiseus* with what appears to be an entire shed skin encircling the upper rim of the nest. Use of snake skin by other birds is also known; most, if not all, species of *Myiarchus* flycatchers in the New World use it as nest-lining material (Skutch 1960; Bent 1963; Lanyon 1978, 1982), and it may be common in other passerines as well (Bent 1963).

The chalk and mammal scats are probably eaten by females as sources of nutrients. The primary inorganic minerals in eggshells are calcium, magnesium, phosphorus, iron, and sulphur (Romanoff and Romanoff 1949). The sample of chalk that was analyzed had substantial concentrations of four of these five minerals. Given that as much as 75% of the mineral, particularly calcium, content of eggs comes from a bird's diet (Comar and Driggers 1949), eating the chalk could certainly benefit females during egg production. Females supplementing their breeding season diet with sources of calcium, e.g., bones, is known from other passerines (Payne 1972, MacLean 1974) and may be widespread. In this regard, it is interesting to note that the shells of land snails, another possible source of calcium, were fairly common in the forest on Mount Missim but were only rarely found at the males' court sites. Despite its potential importance, however, chalk was relatively rare at courts compared with snake skin and mammal scats (Table 1), presumably either because it is rare in the forest or has less importance than we have hypothesized. Females could get bones, and thus calcium, from the scats of the predatory marsupials (e.g., *Dasyurus albopunctatus*), but males were not seen to collect such scats.

With respect to the mammal scats, an interesting possibility is that the females placed them around their nest as an antipredator device. Opossums and other arboreal marsupials would be among the most significant predators on eggs. If individual opossums avoid areas where they detect markings of others, then scats around a

nest or along the branch leading to a nest might reduce marsupial traffic there.

Irrespective of the specific use of the objects by females, it appears that the items provide some benefit to females. The benefit could be relatively minor, as if snake skin is used as nest lining, or potentially important, if chalk is used as a mineral supplement. The most important question is whether the presence of objects at a male's court influences the female's choice of a mate. The data presented here suggest not. The collection of objects did not correlate with the relative mating success of males (Table 3). In one sense, it is this lack of correlation that is intriguing, if objects do in fact benefit females. Perhaps the benefit is not so great as to generate an initial linking between the objects and preferences for mates. There may be an indirect relationship between matings and objects, however, given that the objects appear to influence the length of female visitations (Table 3), which itself is correlated with male mating success (Pruett-Jones and Pruett-Jones, unpubl.). This indirect benefit to males—increasing their exposure to females—may explain why males collect the objects at all if it does not increase their probability of mating.

It is possible that the collection of objects originated in ancestral *P. lawesii* populations which were presumably monogamous and exhibited biparental care (Gilliard 1969, Schodde 1976). If, in the ancestral species of *P. lawesii,* shed snake skin, mammal scats, and chalk were used in nesting or as nutrients, both males and females may have collected them. In the course of evolution of a promiscuous mating system, indirect benefits to males may have been sufficient for the behavior to be retained.

Males may rub the objects on the display perch to make the perch smoother or to increase its visibility or conspicuousness. In the instances where males marked their perch with chalk, the perch was much more noticeable (at least to us). If the objects have parasites on them, rubbing may also reduce the level of parasites. Males probably tear the snake skin into smaller pieces to lessen the possibility that a single female can easily take it all.

The collection of court objects by *P. lawesii* is similar to the collection of bower decorations in bowerbirds in that both behaviors involve manipulation of objects by males that display terrestrially. Gilliard (1963, 1969) suggested that the evolution of bower building arose through intermediate stages in which males first collected objects unrelated to bower construction. It is possible that the collection of court objects in *P. lawesii* represents such an intermediate stage. The important difference between the collection of court objects and the use of bower decorations is that for bowerbirds, the decorations appear to be the focus of male-male competition and female choice (Borgia 1985, Borgia and Gore 1986). This is not the case in *P. lawesii,* the indirect aspects of court objects and matings notwithstanding. Some other differences are that bower decorations are not taken by females, male bowerbirds show strong color preferences in which items they collect, and in some cases the decorations are incorporated into the males' displays (Gilliard 1969; Diamond 1982, 1986; Pruett-Jones and Pruett-Jones 1985).

Our observations have raised a number of important questions which will require experimentation with captive birds to answer. For example, if female *P. lawesii* will breed in captivity it would be interesting to offer them snake skin to see if it is incorporated into their nest. Also, females could be offered chalk and/or eggshells to see if they will, in fact, eat these items. Although much of our discussion is speculative, we believe the objects will be shown to be important with respect to nesting biology of females. Assuming so, this behavior will add yet another dimension to the diversity of mating patterns in lek-breeding birds of paradise and another intriguing similarity between birds of paradise and bowerbirds.

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