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Reproduction by Captive Unplumed Male Lesser Bird of Paradise *Paradisaea minor*: Evidence for an Alternative Mating Strategy?

Mark S. Laska^{1,3}, Michael Hutchins^{2,4}, Christine Sheppard², Wendy Worth², Kurt Hundgen² and Don Bruning²

¹ Biology Dept., Fordham University, Bronx NY, USA 10458

² New York Zoological Park, Bronx NY, USA 10460

³ Present address: Graduate Program in Ecology and Evolution, Nelson Hall, Rutgers, The State University of New Jersey, Piscataway NJ, USA 08855-1059

⁴ Present address: AAZPA Conservation Center, 7970 Old Georgetown Rd., Bethesda MD, USA 20814

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Birds of paradise (Paradisaeidae) have become an important focus for testing current theories regarding sexual selection and mate choice (Beehler & Foster 1987). In the genus *Paradisaea*, the primary mating system is the lek. Colorfully plumed males gather in groups to perform elaborate courtship displays (Gilliard 1969). Females are attracted to these communal display arenas where they assess males and select a mate (Emlen & Oring 1977). Although males in full plumage gain the majority of copulations (Beehler 1983, 1988), it is known that females will occasionally mate with unplumed males (LeCroy *et al.* 1980; LeCroy 1981). The documentation of successful breedings by an unplumed male captive Lesser Bird of Paradise *Paradisaea minor* at the New York Zoological Park has caused us to speculate that wild males may delay the development of mature plumage as an alternative mating strategy. At the

very least, such males could be successful breeders when engaging in matings.

At least eight species of birds of paradise exhibit lek mating systems (Beehler & Pruett-Jones 1983). Elaborate male plumage is thought by many to be a result of runaway sexual selection, females preferring to mate with fully-plumed males (Diamond 1986). For a review of current sexual selection theory see Borgia (1987). Although often debated (LeCroy 1981; Beehler & Foster 1987; Beehler 1988), it is widely believed that one of the primary characteristics of lek systems is that the female has the ability to choose a mate (Bradbury 1981; Bradbury & Gibson 1983). However, in birds of paradise, the precise criteria upon which a female bases her decisions remain unknown (Diamond 1986).

Display by unplumed presumed males has been reported for most species of *Paradisaea* and it is not un-

common for such birds to attend leks along with plumed males (LeCroy 1981). LeCroy (1981) documented mountings by unplumed presumed males among free-living Goldie's Bird of Paradise *P. decora* and suspects they occur in all species of lek-forming *Paradisaea*. The occurrence of this behavior raises the question as to why females should choose to mate with unplumed males. Moreover, with the exception of a single occurrence in *P. raggiana* (Delacour & Mayer, cited in Gilliard 1969), definitive proof of the sexual maturity of unplumed males is lacking.

Methods

The New York Zoological Park (NYZP) maintains eight Lesser Birds of Paradise, in an off-exhibit propagation building (Hundgen & Bruning 1988; Hundgen *et al.* 1990). The primary breeding group consists of one female and two unplumed males. The female arrived in New York in January 1983 and the males arrived in October 1987. The males were probably hatched in the late summer of 1985 and were estimated to be approximately 4.5 years of age at the time of the fertilisations. These males resemble females, except that the upper one third of their breast shows the beginning of a light brown coloration. The lower two-thirds of the breast are a faint yellow, with most of the color being concentrated under the wings. The birds' flank plumes are only about 3 cm long. This contrasts with fully-plumed males whose upper breast feathers are russet brown, and whose lower breast consists of long (20–25 cm), filamentous plumes that are a deep yellow at the base and are white at the tips (Cooper & Forshaw 1977).

The observations reported here are the results of an ongoing study of aspects of behaviour, husbandry, and captive management begun in February 1988 (Laska 1990).

Results

The NYZP female laid 20 eggs over seven seasons but only three (15%) were fertile. Her first fertile egg resulted from copulations with a fully-plumed male that died in July 1986. This egg hatched on 17 May 1986, but the chick only survived four days. Since this time, there have been no plumed males in the collection and subsequent fertile eggs were the result of matings with one of the unplumed males. Keepers observed copulations between the female and this male on three occasions (12, 13, and 15 January 1990). The first fertile egg

produced in 1989 resulted in a dead embryo. The second fertile egg was laid on 17 January 1990 and hatched on 4 February, after an 18-day incubation period. This chick survived 134 days until 17 June 1990 when it died of unknown causes. This is the first evidence that unplumed male *P. minor* are capable of successful reproduction.

Discussion

In some birds of paradise, males may take up to seven years to obtain full adult plumage (Cooper & Forshaw 1977) — a comparatively long time for a passerine. Although not yet confirmed by field data, males may have to wait an additional seven or more years before attaining entry to and dominant status in a lek (B. Beehler pers. comm.). Currently, there are four theories which might explain this phenomenon: (1) the presence of dominant males may inhibit plumage development in subordinates (LeCroy 1981); (2) the metabolic cost of growing and maintaining mature plumage may be high, and only older males may be able to meet the energetic demands (Halliday 1987); (3) due to intense intrasexual competition, it may take years before a male is experienced enough to obtain entry to and status within a lek (Beehler & Foster 1987); and (4) due to more cryptic coloration, individual survival is increased at the expense of reproduction while the bird is young (Butcher & Rohway 1987 and references cited therein). Here we offer an additional explanation, based on alternative mating tactics.

During the course of an eight-month, 154-hour study of captive Lesser Bird of Paradise social behaviour conducted in 1988 (Laska 1990), display behaviours of the NYZP unplumed males were compared to those of wild mature males as described by Beehler (1988), Frith (1981) and LeCroy (1981). The NYZP males were found to show virtually the entire spectrum of display behaviour in both the presence and absence of the female. It is likely that forced proximity and absence of plumed males led to the captive female copulating with unplumed males. We speculate that performance of 'correct' courtship displays are adequate cues for female mate choice, not only in fully-plumed males, as suggested by Frith (1981), but also in unplumed males in the absence of fully-plumed males (see also Foster 1987).

Because competition for mates is intense in lek systems, alternative or opportunistic mating strategies may have evolved. In one scenario, by remaining outside or

on the periphery of a lek, so-called 'satellite' males — some of which may be unplumed — can avoid competition with dominant males but at the same time occasionally gain a copulation. Such tactics have been documented in a wide variety of vertebrates (Rubinstein 1982; Oring 1982).

A complementary tactic may be to delay the development of adult plumage, yet be physiologically capable of producing sperm. There are costs associated with the development of adult plumage. For example, bright, conspicuous feathers may increase vulnerability to predation (Zahavi 1975). The energetic cost of producing sperm is low, whereas the production of exaggerated feather structures may be costly. Thus, an unplumed male can be reproductively successful without incurring the costs associated with mature plumage. Conversely, such a male is unlikely to have any reproductive success on a lek, since it must compete with plumed males, many of which are unable to obtain matings (Beehler 1983). Thus, dominant males may not view unplumed males as threatening competitors. These unplumed males may remain on or near a lek and copulate opportunistically when they encounter a receptive female.

Certain demographic or ecological conditions may result in female selection of unplumed males. For example, in some habitats, leks may be so dispersed, that females have difficulty locating them (Healy 1978; Oring 1982; Beehler 1988). This situation may be further accentuated by human predation on fully plumed males. Healy (1978) stated that '... display trees are not necessarily abandoned if all mature males are shot. Though females may not mate with subadult males when mature males are present, they may do so where display trees are widely spaced and mature males are locally rare.' Additionally, Kwapena (1980) noted that fully-plumed males are often hunted extensively, while unplumed males and females are not. Indeed, Diamond (1972, comm. to Kwapena 1980) speculated that species abundance may not be affected if unplumed males can mate successfully with females and plumed males are removed from a population through hunting. That one unplumed captive male Lesser Bird of Paradise was physiologically capable of reproduction is evidence that alternative strategies may exist.

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The Status of the Black-browed Albatross *Diomedea melanophrys* at Heard Island

R.J. Kirkwood¹ and P.J. Mitchell²

¹ Department of Parks, Wildlife and Heritage, P.O. Box 44A, Hobart, Tas. 7001

² Regional Veterinary Laboratory, Bairnsdale, Vic. 3875

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The Black-browed Albatross *Diomedea melanophrys* is abundant in the Southern Ocean and has a circum-polar distribution (Tickell 1976). Two subspecies are recognised: *D. m. impavada*, which breeds only on Campbell Island, and *D. m. melanophrys*, which breeds in the Atlantic, west Pacific and Indian sectors of the Southern Ocean (Tickell 1976; Croxall *et al.* 1984). Colonies of *D. m. melanophrys* at Heard Island, south of the Antarctic Convergence in the Indian sector of the Southern Ocean, were first reported in 1947 (Downes *et al.* 1959). Since then, the colonies have been visited irregularly. This paper summarises the information gathered, presents new data collected during the 1987-88 austral summer and discusses parameters affecting the current status of the population on Heard Island.

Breeding biology

Immature Black-browed Albatrosses forage at sea year-

round and start returning to breeding sites as seven-year-olds, but it is several more years until they breed. On maturing, the adults breed annually and raise a maximum of one chick per pair per year (Tickell & Pinder 1967, 1975). Individuals can survive to at least 29 years of age (Copson 1988). During the breeding season, the nest site is occupied for approximately seven months (Tickell & Pinder 1975). For the remaining five months of the year, adults forage at sea, generally over continental-shelf waters (Weimerskirch *et al.* 1985). Although the Black-browed Albatross is considered faithful to its nuptial site, the resighting of an incubating adult at Heard Island which had been banded as a chick on the Kerguelen Islands (360 km to the north-west) (Woehler 1989) indicates that there is some mixing between populations.

Breeding chronology and breeding success at islands varies depending on location. At islands that lie