Distinctive courtship phenotype of the Vogelkop Superb Bird-of-Paradise *Lophorina niedda* Mayr, 1930 confirms new species status

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The birds-of-paradise (Aves: Paradisaeidae) are a quintessential example of elaborate ornamental diversification among animals. Ornamental evolution in the birds-of-paradise is exemplified by the presence of a highly integrated courtship phenotype, which is the whole package of plumage ornaments, behaviors and sounds that each species uses during courtship. Characterizing a species' courtship phenotype is therefore a key part of evolutionary and taxonomic investigation in the group. With its unprecedented transmogrification from bird-like form into something abstract and otherworldly, the courtship phenotype of the Superb Bird-of-Paradise, *Lophorina superba,* is one of the most remarkable of all. Recent research by Irestedt et al (2017) suggests that the genus *Lophorina* is not a single species but is likely a complex of three allopatric species spanning the island of New Guinea: *L. niedda* in the Bird's Head Peninsula of the west, *L. superba* throughout the central cordillera and *L. minor* in the Papuan Peninsula of the east. Of these, *niedda* is the most phenotypically divergent with plumage traits hypothesized to possibly produce differences in ornamental appearance during display. However, the whole courtship phenotype of *niedda* has not been documented and so the actual extent of differences in ornamental appearance during courtship remain unknown. Here we analyze the first audiovisual recordings of *niedda* and compare its courtship phenotype with *superba* to test the hypothesis of potential differences in ornamental appearance. Our main goals are to: 1) provide the first description of the courtship phenotype of *niedda* in the wild, 2) determine if and how the *niedda* courtship phenotype differs from *superba* and 3) evaluate any uncovered differences in light of *niedda's* newly recognized species status. Our secondary goal is to provide a more thorough characterization of courtship phenotype diversity within the genus *Lophorina* to facilitate future comparative study within the genus and family. Results show that the *niedda* courtship phenotype differs substantially from *superba* in numerous aspects of ornamental appearance, display behavior and sound.

We highlight six key differences and conclude that the new species status of *niedda* is corroborated by the distinctly differentiated ornamental features documented here. With full species status, *niedda* becomes the fourth endemic bird-of-paradise to the Bird's Head region of Indonesian New Guinea (i.e. the Vogelkop Peninsula), a fact that underscores the importance of this region as a center of endemic biodiversity worthy of enhanced conservation protection.

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12 **ABSTRACT**

13   The birds-of-paradise (Aves: Paradisaeidae) are a quintessential example of elaborate

14 ornamental diversification among animals. Ornamental evolution in the birds-of-paradise is

15 exemplified by the presence of a highly integrated courtship phenotype, which is the whole

16 package of plumage ornaments, behaviors and sounds that each species uses during courtship.

17 Characterizing a species' courtship phenotype is therefore a key part of evolutionary and

18 taxonomic investigation in the group. With its unprecedented transmogrification from bird-like

19 form into something abstract and otherworldly, the courtship phenotype of the Superb Bird-of-

20 Paradise, *Lophorina superba,* is one of the most remarkable of all. Recent research by Irestedt et

21 al (2017) suggests that the genus *Lophorina* is not a single species but is likely a complex of

22 three allopatric species spanning the island of New Guinea: *L. niedda* in the Bird's Head

23 Peninsula of the west, *L. superba* throughout the central cordillera and *L. minor* in the Papuan

24 Peninsula of the east. Of these, *niedda* is the most phenotypically divergent with plumage traits

25 hypothesized to possibly produce differences in ornamental appearance during display. However,

26 the whole courtship phenotype of *niedda* has not been documented and so the actual extent of

27 differences in ornamental appearance during courtship remain unknown. Here we analyze the

28 first audiovisual recordings of *niedda* and compare its courtship phenotype with *superba* to test

29 the hypothesis of potential differences in ornamental appearance. Our main goals are to: 1)

30 provide the first description of the courtship phenotype of *niedda* in the wild, 2) determine if and

31 how the *niedda* courtship phenotype differs from *superba* and 3) evaluate any uncovered

32 differences in light of *niedda's* newly recognized species status. Our secondary goal is to provide

33 a more thorough characterization of courtship phenotype diversity within the genus *Lophorina* to

34 facilitate future comparative study within the genus and family. Results show that the *niedda*

35   courtship phenotype differs substantially from *superba* in numerous aspects of ornamental

36   appearance, display behavior and sound. We highlight six key differences and conclude that the

37   new species status of *niedda* is corroborated by the distinctly differentiated ornamental features

38   documented here. With full species status, *niedda* becomes the fourth endemic bird-of-paradise

39   to the Bird's Head region of Indonesian New Guinea (i.e. the Vogelkop Peninsula), a fact that

40   underscores the importance of this region as a center of endemic biodiversity worthy of enhanced

41   conservation protection.

43   **INTRODUCTION**

44   The birds-of-paradise (Aves: Paradisaeidae) have evolved some of the most elaborate

45   diversification in ornamental mating displays among animals (Frith and Beehler 1998, Laman

46   and Scholes 2012). A key innovation behind ornamental diversification in the birds-of-paradise

47   is the evolution of a functionally integrated *courtship phenotype* (Scholes 2008a, Ligon et al in

48   prep). A species' courtship phenotype is the whole package of plumage ornaments, behaviors

49   and sounds used during courtship. In males, it encompasses the portion of the phenotype that is

50   evaluated by females during courtship and in females it is the portion devoted to mate evaluation

51   and selection (Bostwick et al 2017). Characterizing a species' courtship phenotype is an

52   important part of understanding evolutionary patterns and taxonomic assessment in the birds-of-

53   paradise (Scholes 2008b, Scholes et al 2017a, Scholes et al 2017b, Ligon et al in prep).

54   Among the approximately 40 species of birds-of-paradise, one of the most remarkable

55   male courtship phenotypes is that of the Superb Bird-of-Paradise, *Lophorina superba* (Frith and

56   Frith 1988, Laman and Scholes 2012). Most of what is known about courtship in *L. superba*

57   comes from older descriptions of captive birds (Manson-Bahr 1935, Morrison-Scott 1936, Seth-

58   Smith 1936, Timmis 1968) and two accounts of wild birds from the Adelbert Range (Frith and

59   Frith 1988) and the central cordillera of western Papua New Guinea (Whiteside and Feignan

60   1998). From these sources and film footage of *L. superba* from near Tari, Papua New Guinea

61   obtained for the 1996 documentary film *Attenborough in Paradise,* Frith and Beehler

62   synthesized all knowledge of courtship and mating behavior for *L. superba* (Frith and Beehler

63   1998). The picture that emerged revealed two basic types of courtship display typically given

64   from a horizontal free fall in the forest understory: a suite of relatively simple behaviors called

65   *initial display activity* and the iconic transmogrifying display, called the *high intensity display,*

66   which features a highly specialized ornamental nape cape that is spread laterally to form a super

67   black (McCoy et al 2018) oval-shaped ruff that surrounds the entire head and upper body (Frith

68   and Beehler 1998). This otherworldly display has been likened in appearance to a black and blue

69   bouncing "smiley" face-like form (Laman and Scholes 2012).

70   Historically, the genus *Lophorina* has been treated as a single polytypic species with

71   populations extending throughout mid-montane New Guinea from the Bird's Head (Vogelkop)

72   Peninsula in the west, through all of the central cordillera and to the Papuan Peninsula in the east

73   with isolated populations in the Adelbert Range and Huon Peninsula in the northeast (Frith and

74   Beehler 1998, Frith and Frith 2010). The Bird's Head and Papuan Peninsula populations exhibit

75   geographic variation in female head color (Cracraft 1992, Frith and Beehler 1998, Pratt and

76   Beehler 2015) and the Bird's Head population has minor variation in male ornamental plumage –

77   i.e. no black spots on the feathers of the breast shield ornament (Cracraft 1992, Pratt and Beehler

78   2015). Recently, the Bird's Head population has also been identified as being vocally distinct

79   from the others, but comparative acoustic details have not yet been examined (Beehler and Pratt

80   2016).

81   Recent analysis of DNA sequence data and external morphology from museum

82   specimens suggest that the genus *Lophorina* is likely comprised of three species (Irestedt et al

83   2017). The newly delimited species are: *L. niedda* (with subspecies *niedda* and *inopinata*) in the

84   Bird's Head (Vogelkop) Peninsula, *L. superba* (with subspecies: *superba, addenda* and

85   *latipennis*) throughout the central cordillera, Adelbert Range and Huon Peninsula, and *L. minor*

86   in the Papuan Peninsula (Irestedt et al 2017). Of these, *minor* is the oldest and most genetically

87   divergent lineage, but *niedda* is the most phenotypically differentiated (Irestedt et al 2017). For

88   example, the breast shield feathers of male *niedda* are not as laterally extended as they are in

89   *superba* and *minor* and the outer ornamental cape feathers of *niedda* are more elongated with

90   outwardly-curved and narrowly rounded tips with reduced hair-like fringing (Irestedt et al 2017).

91   As suggested by Irestedt et al 2017, the plumage differences of *niedda* might be expected to

92   produce significant differences in ornamental appearance during display and thereby further

93   validate its newly revised species status, but the courtship phenotype of *niedda* has not been

94   documented in the wild.

95   Here we analyze the first audiovisual recordings of courtship behavior in *niedda* and

96   compare its courtship phenotype with *superba* based on analysis of audiovisual recordings from

97   the Macaulay Library at the Cornell Lab of Ornithology and several documentary films. Our aim

98   is threefold: 1) to provide the first description of the courtship phenotype of *niedda* in the wild,

99   2) test for potential differences in ornamental appearance by determining if and how the *niedda*

100   courtship phenotype differs from *superba* and 3) evaluate any uncovered differences in light of

101   *niedda's* recently recognized species status. An additional goal is to provide a more thorough

102   characterization of courtship phenotype diversity within the genus *Lophorina* to facilitate future

103   comparative study within the genus and among species in the family.

104

MATERIALS & METHODS

106   Field observations and audiovisual recordings of two adult male *L. niedda* were made

107   near the village of Mingre in the Arfak Mountains of West Papua, Indonesia during June-

108   November 2016 and 2017. Multiple simultaneous recordings were made with remotely and

109   manually operated video cameras and audio recorders from within observation blinds. Video was

110   recorded with RED Epic-W Helium and Canon 1DX Mark II cameras fitted with a range of

111   Canon lenses. Audio was recorded using a Marantz PMD 661 and Sennheiser microphones.

112   Focal length, frame size and frame rates of video recordings varied according to the particular

113   camera-lens combination used and particular environmental conditions, but ranged between 50-

114   800mm, 4k-8k and 24-240p respectively.

115   For the video analysis, we screened over 200 raw field recordings using the REDCINE-X

116   Professional and Canon EOS MOVIE Utility software applications. Clips with display behaviors

117   were identified and analyzed frame-by-frame to identify the components of courtship described

118   in the results. Recordings containing practice displays and displays given to females were used

119   for the detailed analysis (Table S1). In total we analyzed 30 practice displays and 14 displays to

120   females. Voucher recordings were archived in the biodiversity media collections of the Macaulay

121   Library at the Cornell Lab of Ornithology (www.macaulaylibrary.org) as accession number

122   ACC4396. Vouchers are cited in the Results using Macaulay Library catalog numbers and can be

123   viewed and/or requested online by searching the Macaulay Library database for catalog numbers

124   ML487530 to 487568 (see also Table S1). Media can also accessed directly using the following

125   URL: https://macaulaylibrary.org/asset/xxxxxx where "x's" are replaced with the desired

126   catalog number.

127   Video frames highlighting important components of the courtship phenotype were

128   extracted as tiff files for creating figures. Modifications to figure images included minor

129   adjustments to improve clarity (e.g. cropping, and small adjustments in levels, brightness and

130   contrast).

131   For the acoustic analysis, archival quality audio files from the Macaulay Library (44khz,

132   16-bit .wav; Table S1) were analyzed with the sound analysis software package Raven Pro

133   version 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA).

134   Video used for the analysis of *L. superba* came from existing archival video and sound

135   recordings from the Macaulay Library (Table S1) of two individual adult male *superba superba*

136   (ML487529, ML487528 and ML458167) and one individual adult male *superba latipennis*

137   (ML458001–458003). All of the recordings with data used in the analysis are cited in the Results

138   and can be viewed and/or requested online via the Macaulay Library database as described

139   above.

140   To broaden our review of potential interspecific variation within *superba*, we also

141   reviewed broadcast video footage obtained by film crews during the production of three

142   documentary films: 1) *Planet Earth* (2006) produced and distributed by the BBC, 2) *Nature:*

143   *Birds of the Gods* (2011) distributed by PBS*,* and 3) *Designed to Dance: Birds of Paradise*

144   (2011) produced by NHK Wildlife. Through communications with the producers and/or with

145   local informants at the filming locations, we know that all three the documentary sequences were

146   filmed near the town of Tari in Hela Province, Papua New Guinea and therefore all represent the

147   subspecies *L. superba addenda*. Clips containing the segments we reviewed and/or full episodes

148   for each film can be viewed online through a variety of sources (e.g. the Planet Earth segment is

149   viewable on the YouTube channel of BBC Earth: https://youtu.be/nWfyw51DQfU and *Birds of*

150   *the Gods* can be viewed on the Nature website: http://www.pbs.org/wnet/nature/birds-of-the-

151   gods-introduction/6229). Due to copyright restrictions, we could not include comparable images

152   of *addenda* in our figures, but unless otherwise noted, the courtship phenotype of *addenda* was

153   found to be identical to those of *superba* and *latipennis* documented here.

154

155   **RESULTS**

156

157   **Initial Display Activity**

158   Our analysis identified three distinct types of initial display activity in *niedda,* which

159   broadly correspond with those of *superba.* In the order in which they occur within the courtship

160   sequence, they are: advertisement, horizontal and pointing displays. Each display is described in

161   detail below. Our analysis did not identify substantial variation in the behaviors, postures and

162   ornaments within the *superba* complex (i.e. among *s. superba, s. addenda* and *s. latipennis)* and

163   so we use *latipennis* as the frame of reference to describe and illustrate the *superba* complex (but

164   see Fig. S1 for details of *superba superba*). Although the three types of initial display activity

165   broadly correspond with those of *superba,* our analysis found that each display of *niedda* has

166   numerous distinctive elements.

167   *Advertisement display* – The central features of this display involve the male excitedly

168   looking up and around from side to side (presumably for a potential mate) while repeatedly

169   flicking his cape forward in front of his head and calling (video vouchers: *superba* ML458000

170   from 0:44 to end; *niedda* ML487533). Upon arrival to the fallen log used for display, the male

171   stands in an alert upright posture with head up, bill forward and tail down (Figs. 1A&B and

172   S1A). The iridescent crown feathers are pushed (anteriorly) toward the bill so that they do not

173   visibly reflect any blue and the entire head appears black from all directions. In this

174   configuration, the ornamental eye-spots are not visible (Figs. 1A&B and S1A&B). In *niedda*, the

175   male typically arrives and departs from his display log by flying low through the forest

176   understory rather than by dropping down from or flying up to the forest canopy immediately

177   above. It is unclear if *superba* does the same with the available data.

178   In *superba,* the main posture of the advertisement display has the nape cape folded over

179   the back and wings, without being spread, such that the terminal tips of the cape reach to, or

180   extend beyond, the base of the tail completely covering the wings (Fig. 1A). In *neidda,* the

181   configuration differs in that the cape sits spread over the upper back such that the terminal tips

182   extend conspicuously to the sides leaving the wing tips and base of the tail uncovered (Fig. 1B).

183   In *superba,* the feathers of the breast shield are held close to the breast and upper body so

184   that, for the most part, the color of the ornament is not visible, especially as viewed from above

185   (Figs. 1A and S1A). One exception is during high-intensity calling in which case the breast is

186   thrust forward causing the breast shield to be pushed outward and made visible (Fig. S1B). In

187   contrast, the breast shield of *neidda* is not held as tightly against the breast and its shorter and

188   narrower lateral tips do not fold back toward the torso as in *superba* (Fig. 1B). The terminal tips

189   of the *neidda* breast shield curve gently outward, which makes the surface of the breast shield

190   slightly concave (Fig. 1B). In both *superba* and *niedda,* the bright yellow color of the gape

191   becomes visible while calling (Figs. 1A&B and S1B).

192   Beyond repeated side to side head turning, the primary movements of the display are a

193   frequent forward "flicking" of the cape, which results from turning the head down and to the side

194   and into a partially open wing in order to perform a rapid false wing preen motion (Fig. 1C&D).

195   The extremely fast movement of the false-preen causes the cape to be quickly flicked forward

196   over the downward turned head in a highly exaggerated and ritualized fashion. In *superba,* the

197   cape largely retains its compact form when flicked forward whereas in *niedda,* the flicked cape is

198   fanned out over the head (Fig. 1C&D).

199   *Horizontal display* – This display is frequently interspersed throughout bouts of the

200   advertisement display and involves the diagnostic adoption of a rigid horizontal posture with the

201   neck outstretched, head lowered, and bill pointing forward to be in line with the body axis (video

202   vouchers: *superba* ML458000 (from 0:33–0:44) and ML458001 (from 0:27–0:34); *niedda*

203   ML487558 from 0:00–0:30). The tail is also lifted so that the whole body forms a horizontal line

204   from tip of the bill to tip of the tail (Figs. 2 and S1C).

205   In most instances, the crown feathers are pushed forward so that the head remains all

206   black in appearance and the ornamental eye-spots are not visible (Fig. 2). However, the eye-spots

207   are occasionally revealed during practice displays or if the bird is about to transition into the

208   pointing display (see below), but then concealed again as the horizontal display continues or the

209   bird ruffles its plumage and returns to a bout of advertisement display.

210   In *superba*, the cape is folded over the back to the base of the tail and is not spread (Figs.

211   2A and S1C). In a position that creates a very different appearance, the cape of *niedda* is held

212   over the back, but spread so that it forms two decurved "wings" that emanate from each side and

213   with tips that droop to the log (Fig. 2B). At times, the cape is partially lifted over the back so that

214   it forms a slight arch behind the head.

215   In *superba,* the longest (lateral) feathers of the breast shield stick out conspicuously to the

216   sides and the central most breast feathers are sleeked against the body so that no color is visible,

217   especially when viewed from above (Fig. 2). Because the body is in elongated horizontal

218   posture, only the blackish underside (ventral side) of the breast feathers project outward. The

219   dark outwardly pointed tips give the appearance of being small pointy "wings" sticking out from

220   the sides of the breast. In *niedda,* the breast shield is also sleeked against the body with no color

221   visible (Fig. 2B), however unlike the arrangement in *superba,* the longest breast shield feathers

222   do not look like "wings" because the wing-like position of the cape obscures them (Fig. 2B).

223   The main movement of the horizontal display is ritualized hopping "run" along the log to

224   change position and orientation (e.g. see ML487557 from 1:16 to end and ML487563 from 0:49–

225   1:29). The hops use both feet at the same time and are typically initiated with a quick wing-flick

226   just prior to the first hop. Although less frequent than in advertisement display, the false wing-

227   preens that cause frontal cape flicking are also given.

228   *Pointing display* – The final display in the initial display activity sequence begins from

229   the posture of the horizontal display, which is the most common, or following an advertisement

230   display vocalization. As the name suggests, the primary feature of this display involves the

231   adoption of a ritualized pointing posture where the bill points skyward as the male's attention is

232   oriented toward a potential, or actual, female (video vouchers: *superba* ML458002 from 0:22–

233   0:53 and ML458003 from 0:50–0:56; *niedda* ML487538 from 0:00–0:03 and ML487540 from

234   2:45–3:28). In *superba*, the body is held in an upright posture, with the upper body lifted from

235   the horizontal to be erect as if the bird is "standing at attention" (Fig. 3A). In *niedda*, body

236   posture is more horizontal with the upper body closer to the log and the head tilted back so that

237   the bill points upward (Fig. 3B and Fig. 4)

238   A key feature of this display is how the feathers of the fore crown are pushed back

239   (posteriorly) to be flattened against forehead the while the hind crown feathers remain pushed

240   forward (anteriorly). This result of this repositioning is that the highly reflective fore crown

241   feathers become visible, changing the appearance from all-black to an iridescent electric blue

242   (Figs. 3 and 4). At the same time, the feathers of the narial tufts are also pushed outward from

243   both sides of the bill, which when aligned with the blue fore crown feathers, and viewed head-

244   on, create the highly distinctive eye-spot ornament. When visible, the eye-spots reflect so

245   brightly relative to the super-black plumage surrounding them that they look somewhat like a

246   pair of headlights (Figs. 3 and 4). It should also be noted that the shape of the erected narial tufts

247   differs between *niedda* and *superba*. In *superba*, the tufts are shorter and thicker, almost wedge-

248   shaped, and do not extend beyond the width of the head (Fig. 3A). In *niedda,* the tufts are narrow

249   and elongate with tips that extend out beyond the width of the head (Fig. 3B).

250   As with the previous behaviors, the arrangement of the cape differs substantially between

251   *superba* and *niedda*. In *superba,* the cape remains tightly folded over the back and is not

252   noticeably spread (Fig. 3A). In *niedda*, the cape is always prominently spread broadly over the

253   back to form the conspicuous decurved wing-like lateral protrusions that are a hallmark of the

254   *niedda* courtship phenotype (Fig. 3B).

255   During the pointing display*,* the breast shield of *superba,* though not as outstretched as in

256   the cape presentation display (see below), is nevertheless quite prominent with its reflective blue

257   color visible (Figs. 3A and S1D). In *niedda*, the breast shield remains sleeked against the breast

258   and largely invisible – its lateral tips concealed (shadowed) by the protruding "wings" of the

259   cape – when viewed from the vantage point of an approaching female (Fig. 4).

260   The main movements during the pointing display involve a ritualized flapping of the cape

261   up-and-down over the back and occasional reorientation along the log to "track" the position of a

262   female as she moves around nearby or approaches. The details of the cape-flap differ between

263   *superba* and *niedda.* In *superba* the cape-flap occurs when the wings are partially lifted and

264   flicked open over the back in coordination with a quick pronounced foot stomp, which causes the

265 cape to flap up-and-down over the back in an exaggerated way such that the terminal tips of the

266 cape feathers rise above the height the of the head (Fig. 3C). In *niedda*, there is a foot stomp, but

267 wings are not flicked open, and are only just raised slightly up-and-down over the back, which

268 results in the cape flapping up, but not as high, and such that the terminal tips of the cape

269 feathers stay at or below the level of the head (Fig. 4D).

270 If the pointing display does not transition into a bout of high intensity display (see

271 below), the fore crown feathers may be pushed forward and back, which causes the eye-spots to

272 disappear and reappear or to "flash" on and off. In that scenario, the breast shield of *superba* is

273 sometimes sleeked against the body again, which cause the reflective blue color to visually

274 "blink off" as well. The cape-flapping may also revert into the pseudo wing-preen cape flicks

275 that are a common feature of the advertisement display.

276 A noteworthy behavior associated with the initial display activity of *niedda* is a leaf

277 tossing behavior (e.g. ML487565 from 1:24–1:35). For this behavior, the male picks up a leaf

278 from the surface of the display log and tosses it into the air in such a way that it often lands on

279 the log nearby. It is unclear if this behavior is a rudimentary form of court clearing behavior

280 similar to that known from *Parotia* species or if it is some form of ritualized visual display like

281 those of *Parotia carolae,* which uses leaves as props during certain displays (Scholes 2006).

282

283 **High Intensity Display**

284 Our analysis identified one high intensity display in both species, which we call the cape

285 presentation display. Our analysis did not uncover substantial variation in the behaviors, postures

286 and ornament forms among *s. superba, s. addenda* and *s. latipennis,* but did find minor variation

287 in cadence of bouncing and snapping sounds (see below). As with the initial display activities,

288   we use *s. latipennis* as the standard frame of reference for the *superba* complex and details on *s.*

289   *superba* are provided in Fig. S1. As with the initial display activities above, our analysis of

290   *niedda* found it to have numerous distinctive elements, which are described below.

291   *Cape presentation display* – The visual form and movements of this display comprise the

292   quintessential features of courtship in the genus *Lophorina* (video vouchers: *superba* ML458003;

293   *niedda* ML487557 and ML487562). When performed to a female, the cape presentation display

294   is typically initiated from the posture of the pointing display – i.e. Fig. 3A *superba* and Figs. 3B

295   and 4 niedda). However, if a female appears suddenly without stopping on a nearby perch on her

296   approach, and during practice displays (no female present), the male will often transition directly

297   into the cape presentation from any of initial display activities (e.g. in ML487557 the pointing

298   display is omitted and the male appears to be caught off guard by the sudden arrival of the

299   female).

300   The cape presentation display begins when the male perceives a female making her

301   approach toward the log. In both *superba* and *niedda,* the cape-flapping of the pointing display

302   (see above) increases in intensity. In *niedda,* the increase is greater as wings are lifted higher

303   over the back and then quickly flicked open and shut in the exaggerated manner of *superba*

304   during pointing (Fig. 5A&B). As in the pointing of *superba*, the cape feathers of *niedda* also flap

305   higher such that the tips exceed the height the of the upward pointing bill (Figs. 5B). In

306   conjunction with the exaggerated wing-flick/cape-flaps, the head is tilted back more sharply, the

307   bill is also opened widely to reveal the bright yellow gape and the breast is thrust forward so that

308   the feathers of breast shield ornament become fully expanded and conspicuous – its reflective

309   surface angled upward toward the approaching female. (Fig. 5A&B). The point at which the

310   male presents his bright yellow gape is the best landmark for identifying of the start of the cape

311   presentation display even though there is often a bout of the exaggerated wing-flick/cape-flaps

312   preceding it.

313   The visual effect of the exaggerated wing-flick/cape-flaps with the breast shield fully

314   revealed is more pronounced in *niedda* than *superba* because of the stark difference in the

315   appearance of the breast shield during the pointing display (e.g. compare breast shield positions

316   in Fig. 3A&B to those in Fig. 5A&B). In both species, the male will reorient himself as needed

317   to track the position of the approaching female and keep his eye-spots and breast shield directed

318   toward the female (e.g. video ML 487530).

319   In *niedda,* bouts of wing-flick/cape-flapping coincide with a distinctive very rapid side-

320   to-side wobbling of the head. As viewed from the front (i.e. the POV of the approaching female)

321   the head wobbling has the effect of making the eye-spots flicker or shimmer. It is possible that

322   the wobbling head movement may also be present in *superba,* but is not discernible from the

323   available data.

324   Next comes the transition into the main part of cape presentation display – i.e. the

325   presentation of the fully opened cape itself. In *superba,* the cape is lifted into its presentation

326   position well before to female arrives on the log (Fig. 5C). In *L. niedda*, the wing-flick/cape-

327   flaps with head wobbles continue for several more bouts after the female has arrived on the log

328   and approaches the male become face-to-face with him (Fig. 5D). As the *neidda* female moves

329   closer, the male will back up slightly and crouch lower before deploying his cape for full

330   presentation (e.g. videos ML487530, ML487538, and ML487562).

331   Although the timing of cape deployment differs between *superba* and *niedda*, the cape of

332   both is lifted into the full display position in largely the same way. First, it is spread wide, fan-

333   like, over the back and then it is raised (anteriorly) and pushed over the head until it creates the

334   super-black (McCoy et al, 2018), slightly concave, cape presentation display form that surrounds

335   the entire head and upper body (Figs. 5E&F and S1E).

336   Once in position however, the form and appearance of the cape presentation phenotype

337   differs dramatically between *superba* and *niedda*. In *superba*, the shape of the cape presentation

338   form is oval – i.e. wider than it is high (Figs. 6A and S1F). In comparison, the shape of the cape

339   presentation form of *niedda* is distinctly crescent shaped – i.e. it has a curved sickle shape that is

340   broad in the center and tapers to a point at each end (Fig. 6B). In *superba*, the border edge of the

341   fully opened cape has a smooth fuzzy appearance (Fig. 6A), which is created by the distinct hair-

342   like fringing along the terminal tips of the individual feathers that comprise the cape. The border

343   edge of the crescent in *niedda* is slightly ribbed and lacks the fuzzy appearance of *superba* (Fig.

344   6B). Correspondingly, the terminal tips of the *niedda* cape feathers have very minor hair-like

345   fringing. The iconic oval shape of *superba* exhibits very little variation within the *superba*

346   complex (e.g. Figs. 6A and S1F for a comparison of *L. s. latipennis* and *L. s. superba* and refer to

347   the documentary films described in the Methods for comparative imagery of *L. s. addenda*).

348   The shape and appearance of the breast shield also differs between the cape presentation

349   phenotype of *superba* and *neidda*. In *superba*, the breast shield is wider with thicker terminal

350   ends that make a relatively flat surface with a fairly straight edge along the top of the ornament

351   (Figs. 6A). In *neidda*, the shorter and narrower terminal tips of the breast shield curve outward so

352   that the surface of the ornament is slightly concave and the top edge is angled downward at the

353   sides (Fig. 6B). This difference results in *niedda* looking like somewhat like "frowning face"

354   whereas *superba* has a "smiling face" look. The "smiling" vs "frowning" face appearance is

355   further enhanced by the difference in how the eye-spot ornaments are created. In *superba*, the the

356   narial tufts are thick and relatively short whereas in *niedda* they are narrow and longer (i.e.

357   extend beyond the width of the head). This difference has the effect of making the eye-spots of

358   *niedda* appear smaller with a straighter line along the top edge, which gives the "eyes" the

359   appearance of having slightly droopy "eyelids" compared with the always larger and circular

360   appearance of the "eyes" in *superba* (Fig. 6A&B). In addition, when alignment of the feathers is

361   not perfect relative to the viewer, the thinner profile of the narial tufts often makes the eye-spots

362   of *niedda* look like they have a thin blue "eyebrow" just above each eye-spots (Fig. partially

363   visible in Fig. 5F). Because the narial tufts fo *superba* are shorter and do not extend over the top

364   margin of the eye-spot, "eyebrows" are never visible nor even possible.

365   Throughout the cape presentation display, the transformed oval-shaped cape presentation

366   form of *superba* is repeatedly lifted up and down, or bounced, with outstretched and bent legs

367   (e.g. ML458003). The repeated up and down movements coincide with a series of alternating

368   shuffle–hop steps to the side, which create the distinct bouncing cadence: up–down shuffle–hop,

369   first to one side and then the other. When a female is present, the male's bouncing shuffle–hop

370   movements revolve around the female in either a semi-circular or full circle path.

371   In *niedda,* the overall appearance of the rotational movement during the cape presentation

372   display is very different from that of *superba.* Instead of the characteristic bouncing of *superba*,

373   the feet of *niedda* move in a faster, more pronounced, side-step motion without bouncing and

374   with no visible up and down movement of the body. This creates the effect of *niedda* appearing

375   to move in a quick but steady glide, rather than bounce, around the female in semi- or full circle

376   (e.g. ML487557 and ML487562).

377   Along with the bouncing (*superba)* or smooth quick (*niedda*) rotational movement of the

378   cape presentation form along the display log, the tail of both species is lifted to about 45 degrees

379   above the plane of the back and rectrices are fanned. The secondary feathers of the wings are

380   spread such that they become partially intertwined with the rectrices (see Fig. S1E). In one

381   explosive motion, the wings are flicked open and shut to the sides, which causes a violent

382   interaction among the secondaries and rectrices. In *superba,* the explosive wing-flicks occur

383   rhythmically with the up–down bouncing movement and coincides with the distinct snapping

384   sounds that are a characteristic acoustic component of the display. In *superba,* the wing-flicks

385   happen on the "down beat" of the bounces, but not on every bounce. In *s. latipennis*, the cadence

386   of snaps and bouncing is down-snap-up, down-snap-up, down-up such that snaps occur in

387   doublets with a distinct pause in between, which sounds like "*snap-snap* (pause) *snap-snap*"

388   (Fig. 7A). In *niedda,* where the rotational movement lacks the bouncing of *superba,* the overall

389   pattern and effect of the wing/tail flicks and snaps is very different because they occur at a

390   regular interval that is not timed with any particular aspect of the rotational movement. The

391   snaps of *niedda* are given at uniform beat of approximately one snap per second for a steady

392   "*snap-snap-snap*" sound (Fig. 8B).

393   In *s. superba,* the cadence of the snapping is more frequent with less obvious

394   choreography among the snaps and bouncing movements. In *s. addenda*, to the extent discernible

395   from the documentary video sources, both the cadence of the bouncing and snapping seems to be

396   more frequent with wing-flicks (and presumably the snaps) occurring with each downward

397   bouncing stroke, "*down-snap-up, down-snap-up, down-snap-up*". In both *niedda* and *superba*,

398   the exact relationship between the wing movement and snapping sound production is unclear and

399   warrants further investigation using high-speed videography.

400   In both *superba* and *niedda,* the cape presentation display ends when the female moves

401   quickly away from the male such that he is unable to continue rotating around her, or when the

402   female solicits copulation. At times the female moves along the log ahead of the male and at

403   other times she will fly away from the log entirely. When females depart, males of both *superba*

404   and *niedda* maintain the full cape presentation posture directed toward her and slowly lower it

405   down over the back to readopt the pointing posture. In *niedda,* as the female departs*,* the male

406   opens his bill to reveal the bright yellow gape once again. This end of display reveal of the gape

407   was not observed in *superba.*

408   If a female solicits copulation (e.g. ML487568 from 0:07–0:17), she beings fluttering her

409   wings as the male rotates around her and then will tip forward with breast low and tail high. At

410   this point, the male circles closely and mounts the female while maintaining the fully open cape

411   posture. The cape is held in the open position during copulation and wing-snaps are given as part

412   of, or just after, the wing flapping that occurs with copulation. After copulation, the male

413   dismounts from the back of the female and resumes the cape presentation display directed at the

414   female (e.g. ML487562). If she departs the log, the male holds the opened cape posture for a few

415   seconds and the slowly lowers it and often returns to the pointing display and sometimes even

416   reverts backwards through the entire sequence from pointing, to horizontal to advertisement

417   displays.

418

419   **Vocalizations**

420   Advertisement vocalizations of both *niedda* and *superba* are phrases of 2–8 notes, with 5

421   notes being the most typical (video vouchers: *superba* ML458003 and *niedda* ML487530; audio

422   voucher: *niedda* ML85763571). While the number of notes is similar in both species, the

423   acoustic quality of *niedda* is very different from the characteristic harsh screeching notes of

424   *superba* (Fig. 7). The basic note structure of *superba* is a harsh raspy screech with little acoustic

425   structure (Fig. 7A). In comparison, the basic note of *niedda* is a high-pitched nasal "*yiap*" sound,

426 which has a piercing whistle-like quality that ascends and descends slightly in frequency (Fig.

427 7B). Note variation in *niedda* includes a version with a more constant pitch (i.e. the frequency

428 does not ascend and/or descend), which sounds more like "*yeep*" instead of the up-and-down

429 frequency of the "*yiap*" notes. Another common variant is slightly higher-pitched and distinctly

430 descending to sound more like "*iap*" rather than "*yiap*" (Fig. 7B). While all three of the common

431 note types can be present in a single phrase, they are usually not given that way. Phrases with a

432 string of 5-6 "*yiap*" notes are the most common.

433

434 **DISCUSSION**

435   The primary purpose of this study was to provide the first description of the courtship

436 phenotype of *Lophorina niedda* in the wild and determine if and how it differs from the courtship

437 phenotype of *L. superba* with special consideration of what differences, if found, would mean in

438 light of *niedda's* newly recognized species status. A secondary goal was to provide a more

439 thorough characterization of courtship phenotype diversity within the genus *Lophorina* in order

440 to facilitate future in-depth comparative study.

441   Our results show that the *niedda* courtship phenotype differs from *superba* in numerous

442 appearance, behavioral and acoustic components. Yet at the same time, the *niedda* courtship

443 phenotype does not contain entirely unique courtship behaviors relative to *superba* – i.e. both

444 have the same higher-order courtship phenotype architecture made up of three relatively simple

445 initial display activities (advertisement, horizontal and pointing displays) and one complex high

446 intensity display (cape presentation). In short, both *superba* and *niedda* share the same

447 underlying courtship phenotype substructure, but differ in many details.

448   The six most diagnostic and noteworthy differences in the courtship phenotype of *niedda*

449   compared with *superba* are: 1) the protruding wing-like position of the ornamental cape during

450   the horizontal and pointing displays (Figs. 2B and 3B); 2) how the breast shield is obscured

451   during the pointing display, which visually emphasizes the "headlight-like" appearance of the

452   eye-spot ornament as viewed by a female observer (Figs. 3B and 4); 3) how during the cape

453   presentation display, the cape is not fully opened until *after* the female approaches at close range

454   on the display log (Fig. 5D); 4) the striking difference in appearance of the fully opened cape

455   presentation form – i.e. the distinctive crescent shape, the ribbed contour, the "frowning face"

456   look of the breast shield and the way in which the eye-spots sometimes have "eyebrows" (Fig.

457   6); 5) how during the during of the cape presentation dance, the male revolves around the female

458   with a smooth quick gliding motion (instead of the characteristic bouncing of *superba*) and with

459   a constant (rather than doublet) wing-snap beat (Fig. 7)*;* and 6) a piercing whistle-like

460   vocalization instead of the characteristic raspy screech of *superba* (Fig. 8).

461   While the differences uncovered here are compelling, there are nevertheless several

462   caveats to be considered. For example, our results are based on relatively low individual sample

463   sizes for both *niedda* and *superba* and therefore may not reflect the full scope of intraspecific

464   variation. However, with the basic framework now in place, future studies will be able to assess

465   this more critically as larger sample sizes are obtained. It should also be noted that while we did

466   not find substantial differences within *superba* (i.e. among *L. s. superba, L. s. addenda* and *L. s.*

467   *latipennis),* sample sizes were limited, based on incomplete primary sources (for *L. s. addenda*)

468   and included an outlying population from the Adelbert Mountains (*L. s. latipennis*) as the main

469   frame of reference for all *superba.* To this last point, given the relatively small and

470   geographically isolated population in the Adelbert Mountains, it is possible that further

471   observations and larger sample sizes could reveal diagnostic differences between it (Adelbert)

472   and cordillera populations. As noted in the Results, there are indications of differences in

473   cadence of wing snaps and bouncing tempo of the cape presentation display among *L. s. superba,*

474   *L. s. addenda* and *L. s. latipennis*. Quantifying these differences requires additional field

475   observation and larger sample sizes.

476   What do the differences uncovered here mean with regard to the species status of *niedda?*

477   We think the distinctive courtship phenotype confirms the conclusions of Irestedt et al (2017)

478   regarding the species status of *niedda.* With the mounting genetic, external morphological and

479   now full courtship phenotype evidence, there can now be little doubt that population of

480   *Lophorina* inhabiting the Bird's Head Peninsula of western New Guinea is a distinct

481   evolutionary lineage that is both geographically and reproductively isolated from the nearest

482   population of *superba* in the Kobowre (Weyland) Mountains of the western cordillera.

483   Furthermore, because all the differences described here are directly related to mating preferences

484   of females and have likely evolved through divergent aesthetic preferences of females, it seems

485   probable that *niedda* and/or *superba* females would not find males of the other type as attractive

486   as males of their own type. However, reciprocal exclusivity in female mating preferences is not

487   required to meet the standards of species delineation in the birds-of-paradise. With the exception

488   of the newly defined *L. minor,* for which there is not enough data to make a determination, bird-

489   of-paradise species are defined by the degree of differences in their courtship phenotypes. In

490   other words, courtship phenotype disparity is the key criterion for species diagnosis in the birds-

491   of-paradise. By this yardstick, *L. niedda* is clearly a distinct species.

492   In addition to characterizing the courtship phenotype of *niedda* for the first time, our

493   results also provide a more complete picture of the *superba* courtship phenotype. For the first

494   time, we document that the initial display activity of *superba* is comprised of three distinct

495   behaviors: the advertisement, horizontal and pointing displays (Figs. 1-3). Previous efforts to

496   describe the displays of *superba* did not differentiate these components into distinct displays

497   even though the basic patterns were described (Frith and Beehler 1998). We also provide the

498   most detailed (and vouchered) descriptions of the *superba* courtship phenotype to date.

499   The findings presented here, along with those of Irestedt et al (2017) indicating that *L.*

500   *minor* is the most genetically divergent lineage in the genus, highlight the need for more

501   investigation of the courtship phenotype of *minor.* Are there differences in the courtship

502   phenotype of *minor* that would shed light on its species status? Currently the only information

503   about the courtship behavior of *minor* comes from incomplete observations of a single captive

504   male that housed in the London Zoological Gardens during the late 1920's and mid 1930's

505   (Manson-Bahr 1935, Morrison-Scott 1936, Seth-Smith 1936). While lacking sufficient

506   description to be fully comparable to the data presented here, it is nevertheless possible to glean

507   several key details. For one, it is evident that *minor* does perform the cape presentation display.

508   However, the presence/absence of initial display activities is unclear from the available data. In

509   fact, when describing the cape presentation display, Manson-Bahr goes as far as stating, "there

510   are no preliminary stages…the display is spontaneous and instantaneous" (Manson-Bahr 1935,

511   pg. 67). While undoubtedly possible, we feel fairly confident that some form of these initial

512   behaviors were either overlooked or lacking by virtue of the conditions of captivity. Regarding

513   the cape presentation display, it is clear from both written descriptions and illustrations that the

514   form of the cape presentation is oval-shaped like *superba,* not crescent-shaped like *niedda,* with

515   visible eye-spots made by the crown feathers (Morrison-Scott 1936, Seth-Smith 1936). The

516   captive *minor* also performed movements that were consistent with the bouncing motions that

517   are characteristic of *superba* during its cape presentation dances (Morrison-Scott 1936). The

518   displays of the captive also included apparent wing movement that produced "clicking" noises

519   (Morrison-Scott 1936). The only possibility of a distinct difference from *superba* that is evident

520   in the descriptions of the captive *minor* is a very clear description of how the eye-spot ornaments

521   have small black spots in their centers, which have the effect of looking like pupils (Morrison-

522   Scott 1936). It was hypothesized that the "pupils" were created through a concave surface to the

523   feathers that create the eye-spots, which seems plausible. However, solid conclusions about the

524   courtship phenotype of *minor* will have to await future field study.

525

526   **CONCLUSIONS**

527   Given the substantial differences in so many aspects of the *niedda* courtship phenotype

528   combined with the acute geographic isolation of *niedda* populations from *superba* populations,

529   leaves little doubt that *niedda* deserves full species status as proposed by Irestedt et al (2017).

530   The species validity *niedda* underscores the importance of Indonesian New Guinea'

531   Bird's Head and Bird's Neck eco-regions (i.e. the Vogelkop Peninsula) as a center of endemic

532   biodiversity that deserves particular attention from the conservation community. Among birds-

533   of-paradise alone, *L. niedda* now joins the three other montane species endemic to the region

534   (*Astrapia nigra, Paradigalla longicuda,* and *Parotia sefilata)* and opens the door for additional

535   systematic scrutiny of the entire avifauna of the Bird's Head (Vogeklop) region, including the

536   other birds-of-paradise at middle and upper elevations (e.g. *Drepanonris albertisi* and

537   *Epimachus fastosus).* Given that the Bird's Head region was the first part of New Guinea to be

538   ornithologically explored, and discovery of new species of birds-of-paradise was the main driver

539   of exploration, it is surprising that the distinctive features of the *niedda* courtship phenotype, and

540   therefore the species status of this unique population, have remained elusive for so long. Yet this

541   fact underscores the need for continued exploration of New Guinea's forests and further

542   systematic investigation of all taxa, including those like the avifauna which are often considered

543   to be relatively well known.

544

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555

556   **REFERENCES**

557   Beehler, B. M. & Pratt, T. K. (2016). *Birds of New Guinea: Distribution, Taxonomy, and*
558   *Systematics*. Princeton University Press, Princeton.
559
560   Bostwick, K. S., Harvey, T. A. & Scholes III, E. (2017). Leveraging diverse specimen types to
561   integrate behavior and morphology. *The Extended Specimen: Emerging Frontiers in Collections-*
562   *based Ornithological Research*. Webster, M. S., ed. CRC Press, Boca Raton.
563
564   Cracraft, J. (1992). The species of the birds-of-paradise (Paradisaeidae): applying the
565   phylogenetic species concept to a complex pattern of diversification. *Cladistics,* 8, 1–43.
566
567   Frith, C.B. & Beehler, B. (1998). *The birds of paradise: Paradisaeidae*. Oxford University Press,
568   Oxford.
569

570   Frith, D. W. & Frith, C. B. (1988). Courtship display and mating of the Superb Bird of Paradise
571   *Lophorina superba. Emu,* 88, 183–188.
572
573   Irestedt, M., Batalha-Filho, H., Ericson, P., Christidis, L., & Schodde, R. (2017). Phylogeny,
574   biogeography and taxonomic consequences in a bird-of-paradise species complex, *Lophorina-*
575   *Ptiloris* (Aves: Paradisaeidae). *Zoological Journal of the Linnean Society*, 181(2), 439–470.
576   Laman, T. & Scholes, E. (2012). *Birds of paradise: revealing the world's most extraordinary*
577   *birds*. National Geographic Books, Washington, D.C..
578
579   Ligon R. A., Diaz, C. D, Morano, J. L., Troscianko, J., Stevens, M. Moskeland, A., Laman, T. G.
580   & Scholes, E. (in submission). Functional Integration of complex courtship signals in the birds-
581   of-paradise. *Nature Communications*.
582
583   Manson-Bahr, P. H. (1935). Remarks on the displays of birds of paradise. *Bulletin of the British*
584   *Ornithological Club.* 56, 63-68.
585
586   McCoy, D., Feo, T., Harvey, T. A. & Prum, R. O. (2018). Structural absorption by barbule
587   microstructures of super black bird of paradise feathers. *Nature Communications*, 9(1), 1–8.
588
589   Morrison-Scott, T. (1936). Displays of *Lophorina superba minor. Proceedings of the Zoological*
590   *Society London.* 1336, 809.
591
592   Pratt, T. K. & Beehler, B. M. (2015). *Birds of New Guinea*. Second Edition. Princeton University
593   Press, Princeton.
594
595   Scholes, E. (2006). Courtship ethology of Carola's Parotia (*Parotia carolae*). *The Auk,* 123(4),
596   967–990.
597
598   Scholes, E. (2008a). Evolution of the courtship phenotype in the bird of paradise genus *Parotia*
599   (Aves: Paradisaeidae): homology, phylogeny and modularity. *Biological Journal of the Linnean*
600   *Society,* 94, 491–504.
601
602   Scholes, E. (2008b). Structure and composition of the courtship phenotype in the bird of paradise
603   *Parotia lawesii* (Aves: Paradisaeidae). *Zoology*, 111, 260–278.
604
605   Scholes, E., Beehler, B. M., & Laman, T. (2017). Taxonomic status of *Parotia berlepschi*
606   Kleinschmidt, 1897 based on analysis of external appearance, voice and behavior (Aves:
607   Paradisaeidae). *Zootaxa,* 4329(6), 560–572.
608
609   Scholes, E., Gillis, J., & Laman, T. G. (2017). Visual and acoustic components of courtship in
610   the bird-of-paradise genus *Astrapia* (Aves: Paradiseidae). *PeerJ,* 5:e3987.
611
612   Seth-Smith, D. (1936). Remarks on the display of Birds of Paradise. *Proceedings of the*
613   *Zoological Society of London.* 1936, 807-808.
614

615   Timmis, W. H. (1968). Breeding of the Superb Bird of Paradise at the Chester Zoo. *Avicultural*
616   *Magazine*. 74, 170-172.
617
618   Whiteside, R. & Feignan, M. (1998). Displays and associated behavior of wild Superb Birds of
619   Paradise *Lophorina superba. Australian Bird Watcher*, 17, 357–363.
620
621

Figure 1

Advertisement display of *superba* and *niedda*.

The central features of this display involve the male excitedly looking up and around from side to side while calling and flicking the cape in front of the head. In *superba* (A), the cape is held folded over the back and wings, without being spread, such that the terminal tips of the cape reach to, or extend beyond, the base of the tail (see arrow). The feathers of the breast shield are held close to the breast so that the color of ornament is not visible. In *neidda* (B), the cape is spread widely over the upper back such that the terminal tips extend conspicuously to the sides (see arrow) leaving the wing tips and base of the tail uncovered. The breast shield is not held as tightly against the breast and its shorter and narrower lateral tips do not fold back toward the torso as in *superba*. The terminal tips of the *neidda* breast shield curve gently outward, which makes the surface of the breast shield slightly concave. The primary movement is a frequent forward "flicking" of the cape, which results from turning the head down and to the side into a partially open wing in order to perform a rapid false wing preen motion. In *superba* (C), the cape largely retains its compact form when flicked forward, whereas in *niedda* (D), the cape fans out distinctively over the head. Image credit/source: (A&C) Edwin Scholes/ML458003 and (B&D) Tim Laman/ML487533.

Figure 2

Horizontal display of *superba* and *niedda*.

This display involves the diagnostic adoption of a low rigid horizontal posture with the neck outstretched, head lowered, bill pointing forward and tail lifted to be horizontal so that the whole body forms a horizontal line from tip of the bill to tip of the tail. Crown feathers are pushed forward so that the head remains all black in appearance and the ornamental eye-spots are not visible. In *superba* (A), the cape is folded over the back to the base of the tail and is not spread. Arrow "C" points to the terminal tips of the cape feathers. The longest feathers in the breast shield of *superba* stick out conspicuously to the sides while the central breast feathers are sleeked against the body so that no color is visible. The dark outwardly pointed tips give the appearance of being small pointy "wings" sticking out from the sides of the breast. Arrow "BS" points to the terminal tips of the breast shield feathers on the bird's right side. In *niedda* (B), the cape is spread widely over the upper back to form a slightly raised narrow crescent with decurved "wings" spread to each side and with tips that droop to the log. Arrow "C" points to the terminal tips of the cape feathers on the bird's right side. The breast shield of *niedda* is sleeked against the body with no color visible. Unlike the arrangement in *superba,* the longest breast shield feathers of *niedda* are not as noticeable because of how they are obscured by the wing-like position of the cape. Image credit/source: (A) Edwin Scholes/ML458003 and (B) Tim Laman/ML487563.
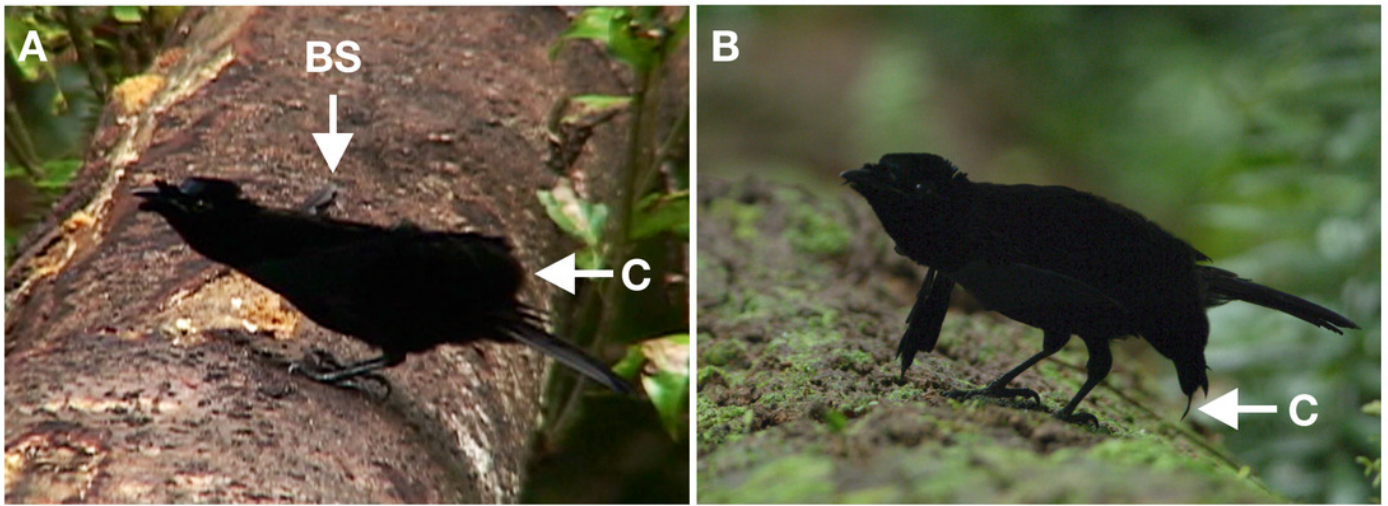
Figure 3

Pointing display of *superba* and *niedda*.

This display involves a ritualized pointing posture where the bill points skyward. The feathers of the fore crown are pushed back against forehead the while the hind crown feathers remain pushed forward, which makes the reflective fore crown visible. The narial tufts are lifted outward from both sides of the bill, which creates the distinctive eye-spot ornament when aligned with the fore crown feathers snf viewed head-on. In *superba* (A), the body is held upright, as if the bird is "standing at attention" with breast shield prominently displayed. Narial tufts are wedge-shaped and do not extend beyond the width of the head. The cape remains folded over the back. In *niedda* (B), the body posture is more horizontal with the head tilted back so that the bill points upward. Narial tufts are elongate with tips that extend out beyond the width of the head. The cape is spread over the back to form the conspicuous decurved wing-like protrusions, which obscure the breast shield. Movements include a ritualized flapping of the cape over the back. In *superba* (C), the cape-flap occurs when the wings are partially lifted flicked open over the back in coordination with a quick foot stomp, which causes the cape to flap up-and-down such that the terminal tips of the cape feathers rise above the height the of the head. In *niedda* (D), there is a foot stomp, but wings are only raised slightly up-and-down over the back, which causes the terminal tips of the cape feathers stay at or below the level of the head. Image credit/source: (A&C) Edwin Scholes/ML458003 and (B&D) Tim Laman/ML487538.
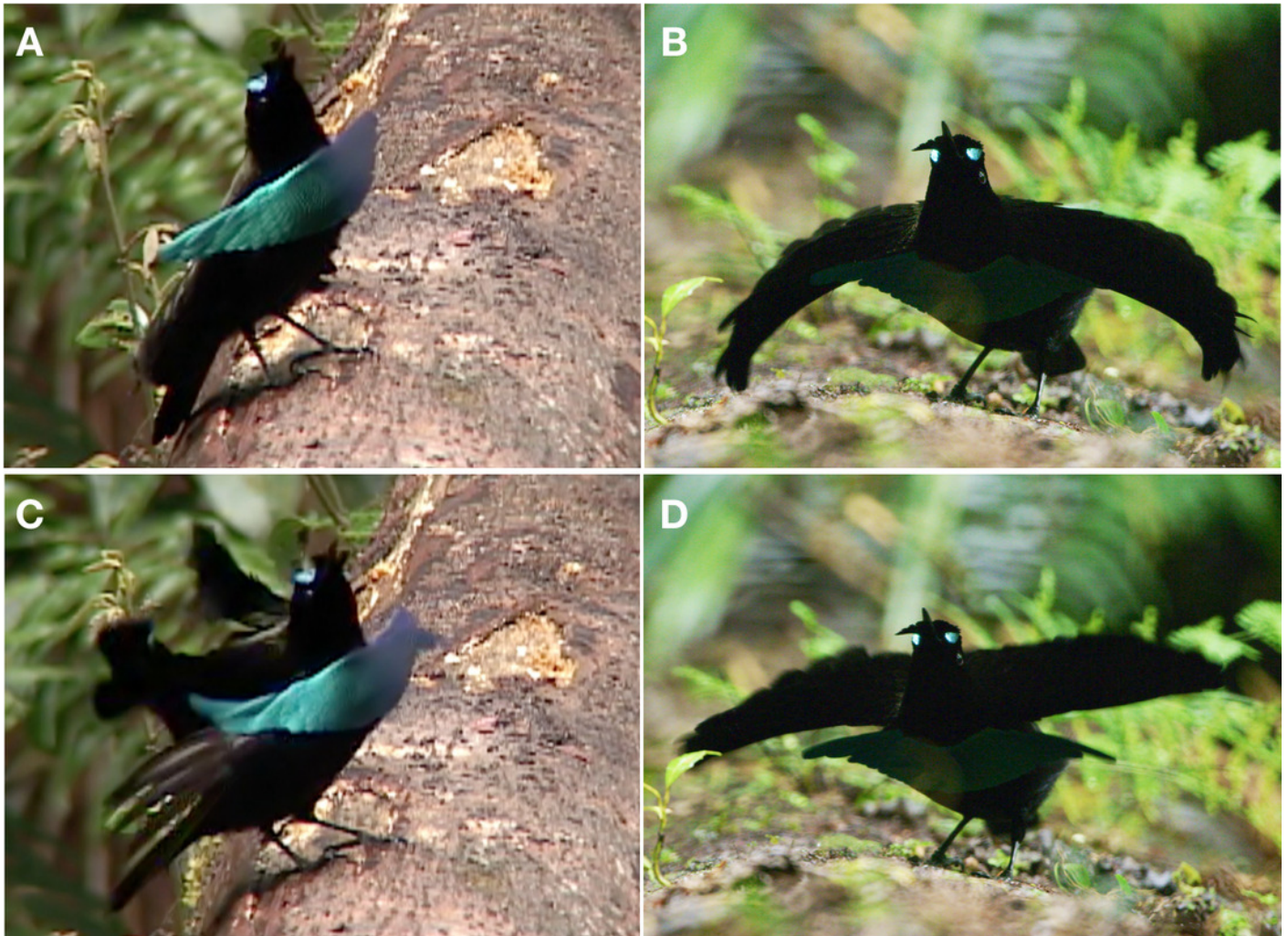
Figure 4

Pointing display of *niedda* as viewed by a female.

The white arrow points to a female plumaged bird (and presumed female) observing the male on his display log. Note how the breast shield remains sleeked against the breast and is effectively invisible – its lateral tips concealed (shadowed) by the protruding "wings" of the cape. In this context, the eye-spots reflect so brightly relative to the super-black plumage of the rest of the male that they look like a pair of headlights "shining" toward the female. This "headlight pose" with the wing-like cape results in a very different appearance from the pointing display of *superba.* Image credit/source: Tim Laman/ML487540.

Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.

Figure 5

Cape presentation display of *superba* and *niedda*.

The visual form of this display is the quintessential feature of courtship in the genus *Lophorina*. In both *superba* and *niedda* (A&B), cape-flapping increases in intensity. In *niedda* (B), the increase is greater because the wings are lifted higher over the back and then flicked open and shut in the exaggerated manner of *superba*. Simultaneously, the breast is thrust forward so that the breast shield becomes fully expanded and conspicuous with its reflective surface angled toward the approaching female. In *superba* (C), the cape is lifted into presentation position before to female arrives on the log. In *L. niedda* (D), wing-flick/cape-flaps continue for several more bouts after the female arrives and before the cape is put into presentation position. The appearance of the cape presentation phenotype differs dramatically between *superba* (E) and *niedda* (F). Image credit/source: (A,C&E) Edwin Scholes/ML458003, (B) Tim Laman/ML487538 (D&F) Tim Laman/ML487557.

Figure 6

Detailed comparison of the cape presentation form of *superba* and *niedda*.

In *superba* (A), the shape of the cape presentation form is oval – i.e. wider than it is high. The edge of the opened cape has a smooth fuzzy appearance, which is created by the distinct hair-like fringing along the terminal tips of the individual feathers that comprise the cape. In *niedda* (B), the shape of the cape presentation form is distinctly crescent shaped – i.e. it has a curved sickle shape that is broad in the center and tapers to a point at each end.mThe contour of the crescent is slightly ribbed and lacks the fuzzy appearance of *superba*. The shape and appearance of the breast shield also differs between the cape presentation phenotype of *superba* and *neidda*. In *superba* (A), the breast shield is wider with thicker terminal ends that make a relatively flat surface with a fairly straight edge along the top of the ornament. In *neidda* (B), the shorter and narrower terminal tips of the breast shield curve outward so that the surface of the ornament is slightly concave and the top edge is angled downward at the sides. This difference results in *niedda* looking like somewhat like "frowning face" whereas *superba* has more of a "smiling face" look. Also, the thinner profile of the narial tufts of *niedda* often makes the eye-spots look like they have thin blue "eyebrows" just above each eye-spots. Because the narial tufts fo *superba* are shorter and do not extend over the top margin of the eye-spot, "eyebrows" are possible. Image credit/source: (A) Edwin Scholes/ML458003 and (B) Tim Laman/ML487563.
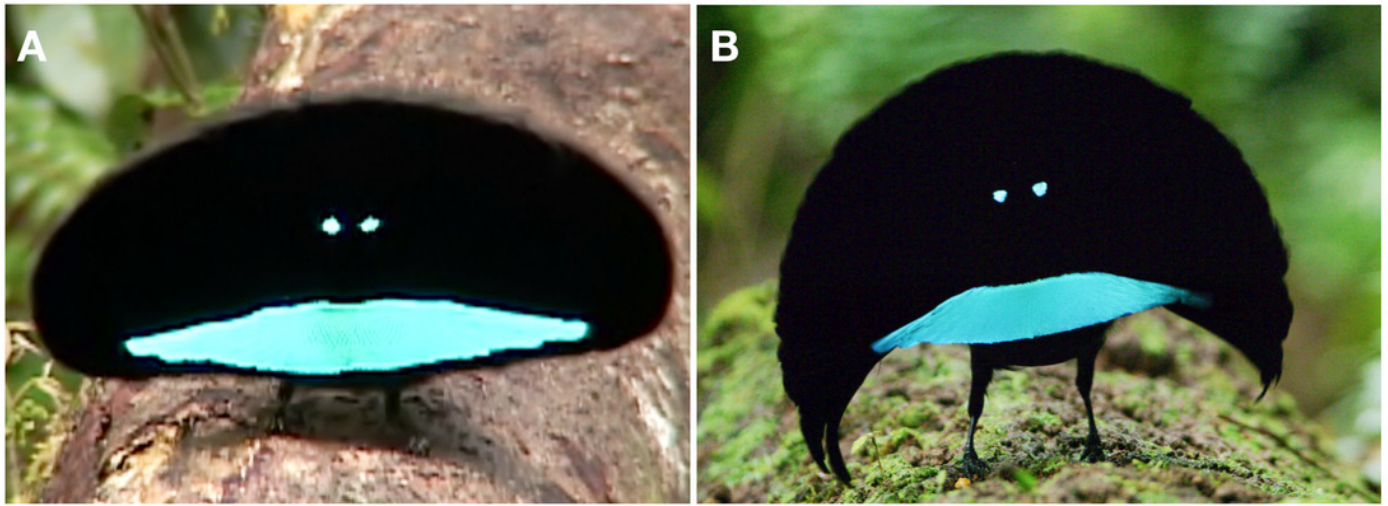
Figure 7

Wing-flick snaps of *superba* and *niedda*.

In *superba* (A), distinct snapping sounds are a characteristic acoustic component of the cape presentation display and occur rhythmically with the up–down bouncing movement on the down beat of the bounces, but not on every bounce. In *superba latipennis*, the cadence of snaps and bouncing is down-snap-up, down-snap-up, down-up such that snaps occur in doublets with a distinct pause in between, which sounds like "*snap-snap* (pause) *snap-snap*". In *niedda* (B), where the rotational movement lacks the bouncing of *superba*, the overall pattern and effect of the wing/tail flicks and snaps is very different because they occur at a regular interval that is not timed with any particular aspect of the rotational movement. The snaps of *niedda* are given at uniform beat of approximately one snap per second for a steady "*snap-snap-snap*" sound. Audio credit/source: (A) Edwin Scholes/ML458003 and (B) Edwin Scholes/ML8576351.
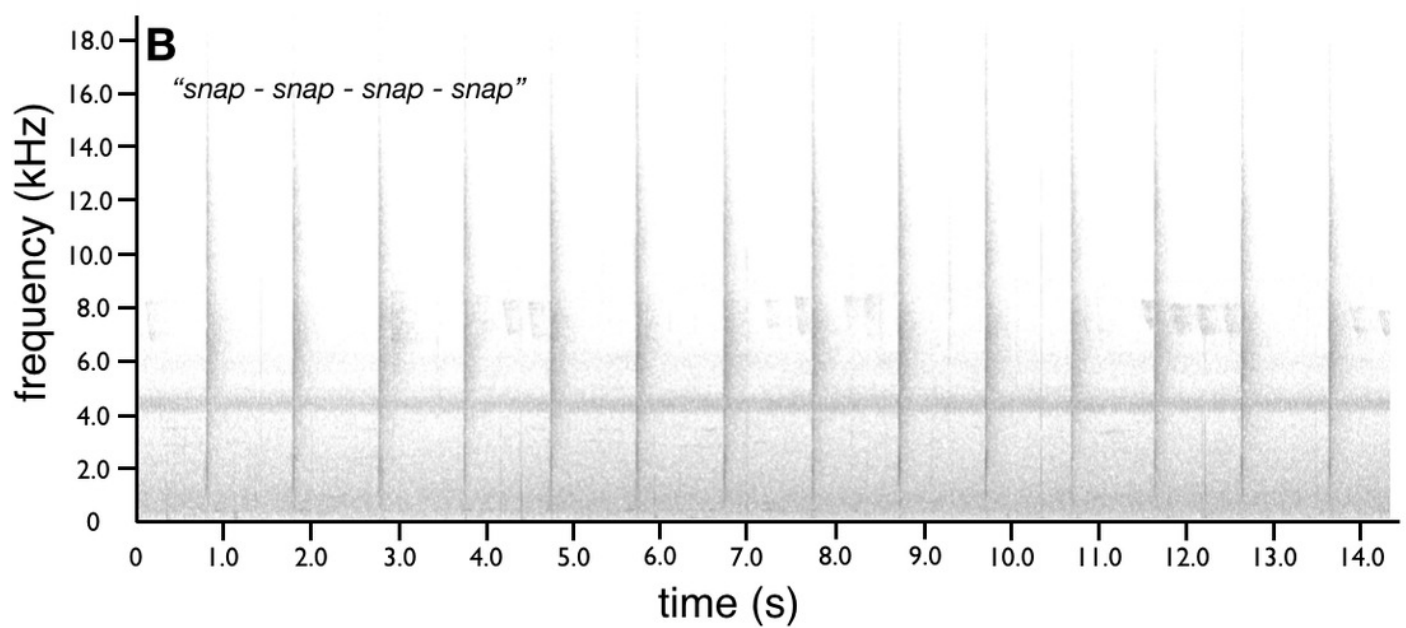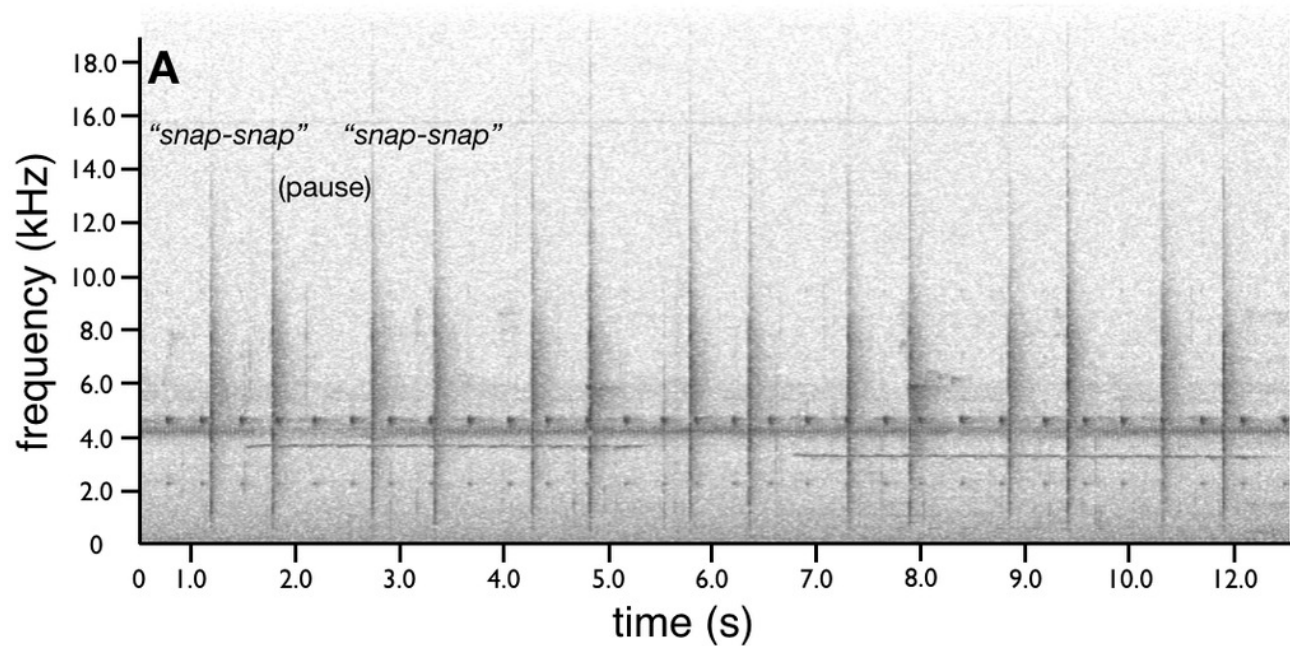
Figure 8

Advertisement vocalizations of *superba* and *niedda*.

Advertisement vocalizations of both *niedda* and *superba* are phrases of 2–8 notes, with 5 notes common. While the number of notes is similar in both species, *superba* (A) gives a characteristic harsh raspy screech. The acoustic quality of *niedda* (B) vocalizations are very different. The basic note of *niedda* is a high-pitched nasal "*yiap*" sound, which has a piercing whistle-like quality that ascends and descends slightly in frequency. Audio credit/source: (A) Edwin Scholes/ML458003 and (B) Edwin Scholes/ML85763571.